CHEMISTRY OF WATER MILFOIL TISSUE: SEASONAL VARIATION IN SUBMERSED APICES

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

The mineral composition of submersed apices in *Myriophyllum heterophyllum* from Lake Winnipesaukee were analyzed from 1976 through 1978. Seasonal changes in ash, phosphorus, sodium, potassium, calcium, magnesium, iron, manganese, zinc and copper were quantified. The magnitude of the seasonal and spatial variations in mineral tissue levels is large. Ash, phosphorus, sodium, potassium, calcium and magnesium vary by a factor (max/min) of 3-5 during an annual cycle. Variations for iron, manganese and zinc are much greater, with max/min ratios of 13-64. Our results question the practicality and validity of reported techniques which use mineral concentrations as an index of nutrient availability and as monitors of aquatic pollutants. We also conclude that inter- and intraspecific comparisons in the chemical composition of aquatic plants should include seasonal analysis on the different plant tissues, if nutrient dynamics and interrelationships of rooted aquatic plants with water and sediment chemistry are to be understood.

INTRODUCTION

Apical tissue is the site of meristematic activity in submersed aquatic macrophytes. Micro- and macroelement requirements for submersed aquatic macrophytes are frequently determined by growing apical sections, harvested from natural waterbodies, in hydroponic growing media (Basiouny, Garrard, and Haller, 1977). A parallel line of research has been done by Gerloff to assay the nutrient status of lakes and streams. Gerloff's tissue analysis technique measures the mineral content of sub-apical sections in submersed macrophytes from the field and compares these values with laboratory established critical levels for maximum biomass production (Gerloff, 1975, 1973; Gerloff and Fishbeck, 1973; Gerloff and Krombholz, 1966). Adams, Cole and Massie (1973) and others have suggested using mineral level measurements in aquatic plant tissues as a technique for monitoring aquatic pollutants because of the plants' ability for luxury uptake.

The importance of natural seasonal changes in the mineral composition of submersed aquatic macrophytes on field samples collected for nutrient and pollution studies is poorly understood. This study quantifies seasonal changes from 1976 through 1978 in ash, phosphorus, sodium, potassium, calcium, magnesium, iron, manganese, zinc and copper in submersed apices of *Myriophyllum heterophyllum* Michx., as a step towards understanding the magnitude of temporal changes in the mineral composition of apical tissue in submersed aquatic macrophytes. This is also the first comprehensive study of mineral concentrations in a submersed macrophyte from a soft-water, New England lake.

METHODS

The apical 5 cm of actively growing submersed stems of *M. heterophyllum* were collected from 14 sample sites in Lake Winnipesaukee and Lee's Pond, New Hampshire, from 1976 through 1978 (Figure 1, Table 1). The apices were rinsed in tap water to remove detritus and epiphytes. The apices were then subdivided into samples, dried for 24 hours at 105°C in a force-draft oven, weighed, ashed for 7 hours at 550°C and reweighed. Five apices constituted an observation and at least triplicate observations a sample. A total of 399 observations were processed and analyzed for ash and nine elements (Table 2) -- 366 from nine major sites and 33 from five minor sites. The minor sites were excluded from the calculations of monthly averages.

The cations Na, K, Ca, Mg, Fe, Mn, Zn, and Cu were extracted by boiling the ash in 50 ml of 5% HCl for 20-30 minutes and then analyzed on a Perkin-Elmer Model 306 atomic absorption spectrophotometer calibrated with standard solutions of each metal. Dilutions with double distilled water were made with the Mg (1:1), Ca (1:1), and K (1:10) samples. A 2% La solution was aspirated with the Ca samples. Phosphorus was determined from the tissue digest, with the colormetric ammonium molybdate and potassium antimonyl tartrate-ascorbic acid reaction. The absorbance was read at 650 nm on a Fisher Electrophotometer with 5 cm cuvets. Percent ash was measured gravimetrically.

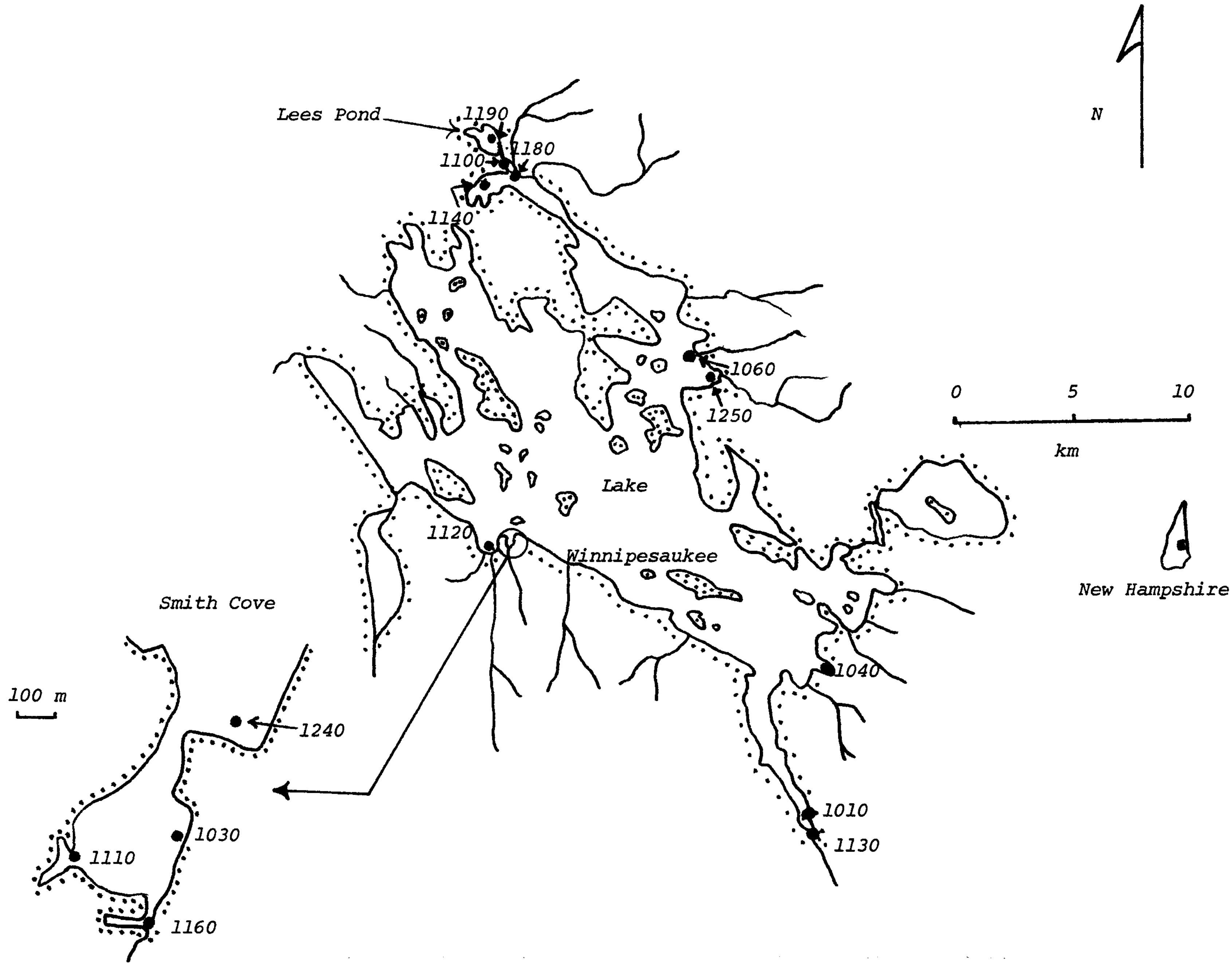


Figure 1. Lake Winnipesaukee study area and location of sampling sites.

Table 1.

Description of Site Locations

Site Number	General Location	Site Description
1010	Alton Bay	E. shoreline, ca. 150 m NE of Merrymeeting R., at public beach
1030	Smith Cove	Ostrand's Marina boatslips
1040	Roberts Cove	Roberts Marina boatslips
1060	Twenty-mile Bay	backwater marsh at mouth of Twenty-mile Brook
1100	Lee's Mill Cove	mouth of Lee's Pond outlet, in Lee's Mill Cove
1110	Smith Cove	Fay's Marina boatslips
1120	Saunders Bay	Gilford Marina boatslips
1130	Alton Bay	Parker's Marina boatslips
1140	Green's Basin	marshy area at N end of Green's Basin
1160	Smith Cove	mouth of Lazy Meadow Brook, adjacent to Gilford Yacht Marina
1180	Lee's Mill Cove	Lee's Mill Cove
1190	Lee's Pond	public boat launch, SE shore of Lee's Pond (Pond 100 m NW of Lee's Mill Cove--L. Winnipesaukee)
1240	Smith Cove	boatslips at Glendale
1250	Nineteen-Mile Bay	backwater marsh of Nineteen-Mile Brook

Table 2. Distribution of the Number of Samples by Site Location and Season.

Date	Station														
	1010	1030	1040	1060	1100	1110	1120	1130	1140	1160	1180	1190	1240	1250	
01/1976	3	–	–	3	–	–	–	3	3	3	–	–	–	–	
02/	2	–	–	1	–	–	–	–	–	1	–	–	–	–	
03/	6	–	–	6	–	–	–	3	3	6	–	–	–	–	
04/	3	–	–	–	–	–	–	–	–	–	–	–	–	–	
05/	6	–	–	–	–	–	–	–	–	–	–	–	–	–	
06/	6	3	–	6	6	3	3	3	5	3	6	3	–	–	
07/	6	6	–	3	3	6	–	–	–	6	3	–	–	–	
08/	3	–	–	3	3	3	–	–	3	3	3	–	–	–	
09/	–	–	–	–	3	–	–	–	3	–	3	–	–	–	
10/	–	–	3	5	3	3	–	–	3	3	3	–	3	3	
12/	–	3	–	3	3	–	–	–	3	3	–	–	–	3	
02/1977	–	3	–	3	3	–	–	–	3	3	–	–	–	–	
03/	–	3	–	3	3	–	–	–	–	3	–	–	–	–	
05/	–	–	–	3	3	–	–	–	–	3	–	3	–	–	
06/	–	3	–	3	3	–	–	–	–	3	–	–	–	–	
07/	–	–	–	–	–	–	–	–	–	–	1	–	–	–	
08/	3	3	–	3	3	–	–	–	–	3	3	3	–	–	
09/	3	3	–	3	3	–	–	–	–	3	2	3	–	3	
10/	–	–	–	–	–	–	–	–	–	–	2	–	–	–	
11/	3	3	–	3	3	–	–	–	–	3	2	3	–	3	
12/	3	3	–	3	3	–	–	–	–	3	–	3	–	–	
03/1978	–	3	–	2	–	–	–	–	–	3	1	–	–	–	
05/	–	3	–	3	3	–	–	–	–	3	4	–	–	3	
06/	3	3	–	3	3	–	–	–	–	3	2	3	–	3	
TOTAL	50	42	3	62	51	15	3	9	26	61	35	21	3	18	399

RESULTS AND DISCUSSION

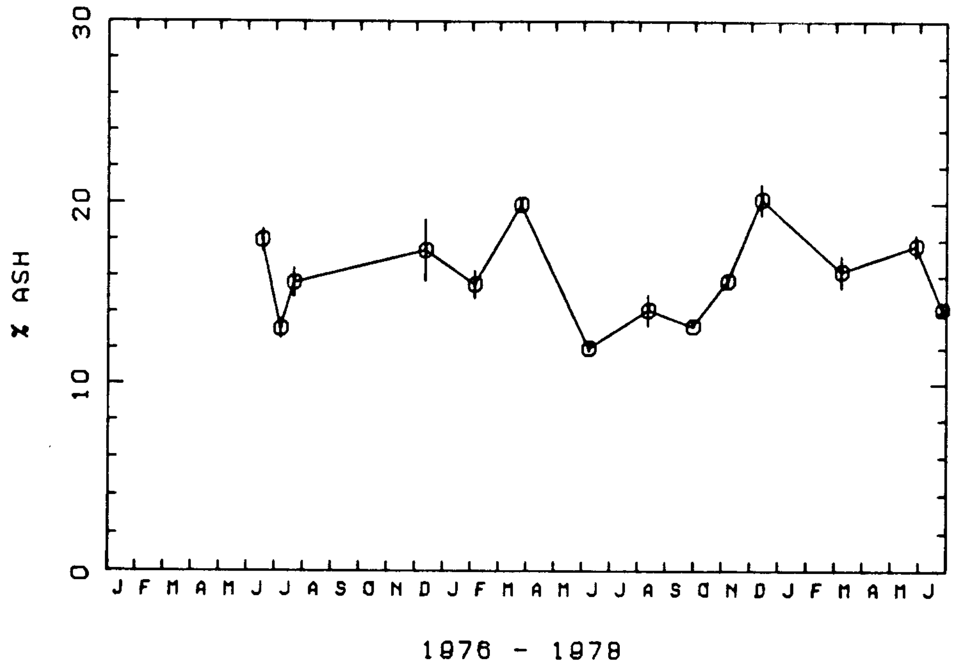
Ash

The nine major sampling sites' means for monthly ash levels ranged from 9.1 to 30.2% dry weight (Figures 2a-e). Increases in ash content from autumn through late winter were common (Figures 2a, 2b, 2d), with maximum concentrations often exceeding 20%. The ash levels of apices from sampling sites proximate to inflowing tributaries were positively correlated with their iron levels (Sta. 1010, df = 14, $r = 0.63$, $p < 0.01$; Sta. 1060, df = 21, $r = 0.59$, $p < 0.01$; Sta. 1160, df = 20, $r = 0.89$, $p < 0.01$).

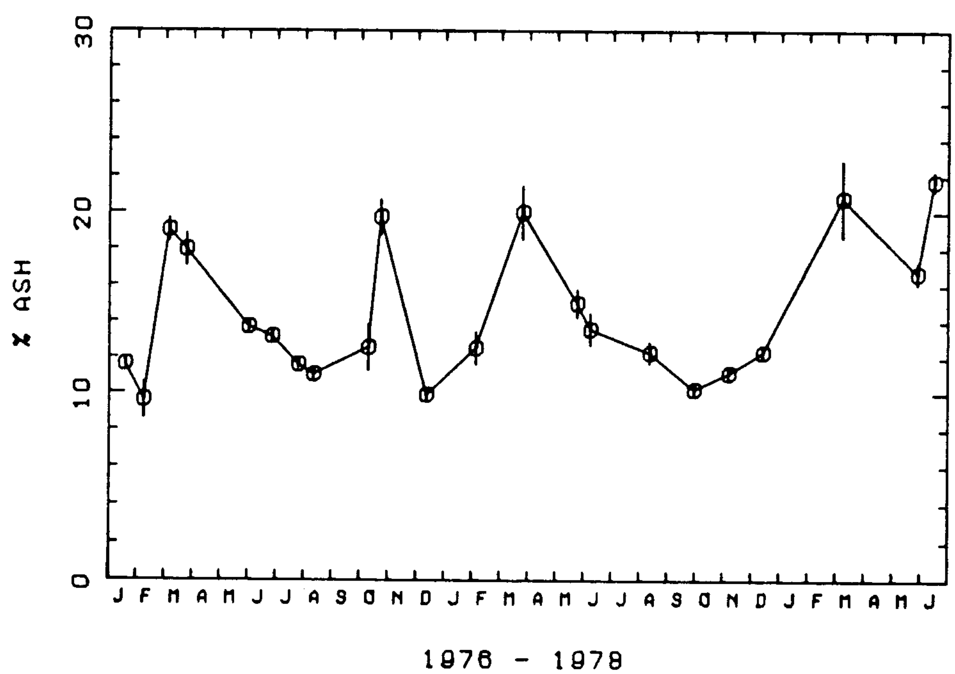
Phosphorus

Phosphorus has been recognized during the past two decades to be a growth limiting nutrient in freshwater systems, as well as the major limiting factor in most cases. The importance of phosphorus in the metabolism of essentially all organisms includes its use as an energy carrier in ATP and as a component of nucleotides in genetic systems. The primary source of phosphorus for water milfoil is generally by uptake from sediments through an extensive system of accessory roots, while some uptake through the epidermis of the stem and leaves occurs depending upon availability (Barko and Smart, in print; Best and Mantai, 1978; Bristow and Whitcombe, 1971; DeMarte and Hartman, 1974).

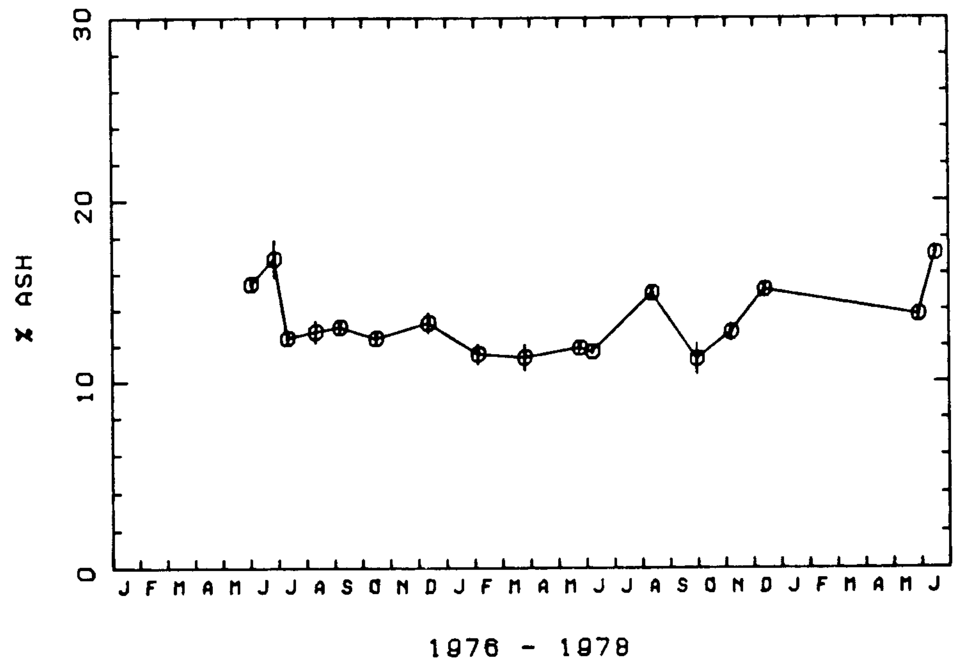
Mean monthly levels of phosphorus in the apical tissue were in the range of 0.3 to 1.1% dry weight at the nine major sampling sites (Figures 3a-e). Seasonal trends in the phosphorus levels were unclear at some of the sites, but the sites at the mouths of tributaries to the lake had pronounced seasonal patterns (Figure 3b). A generalized cyclic pattern of phosphorus concentrations in the apex has a late spring to early summer maximum of 0.6 to 0.7% dry weight and a summer minimum of 0.4 to 0.5% dry weight. Phosphorus levels in the submersed apices generally increased during the late summer through late winter



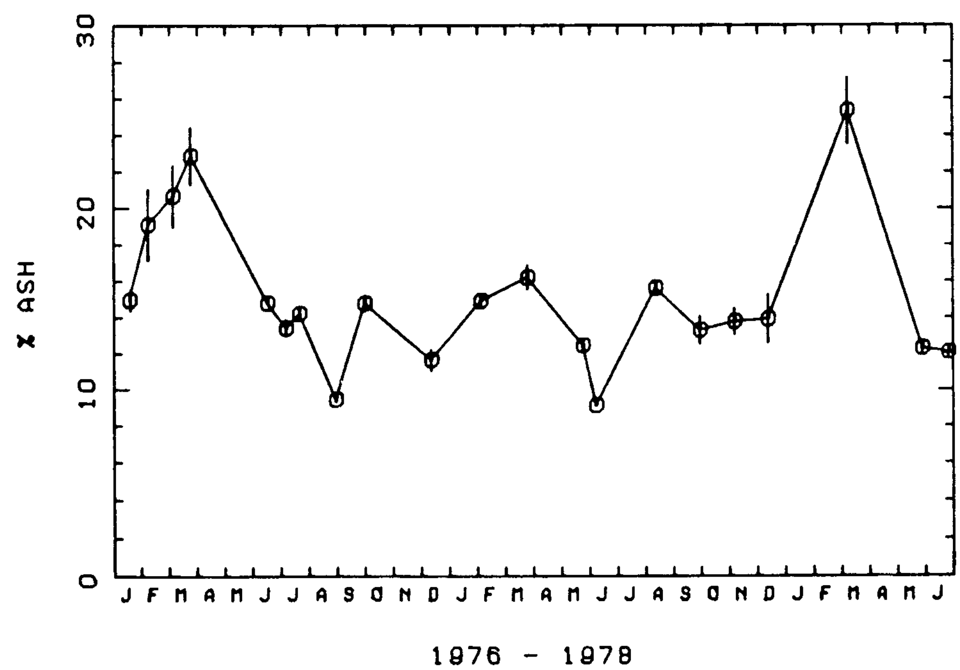
2a. OSTRAND'S MARINA (1030)



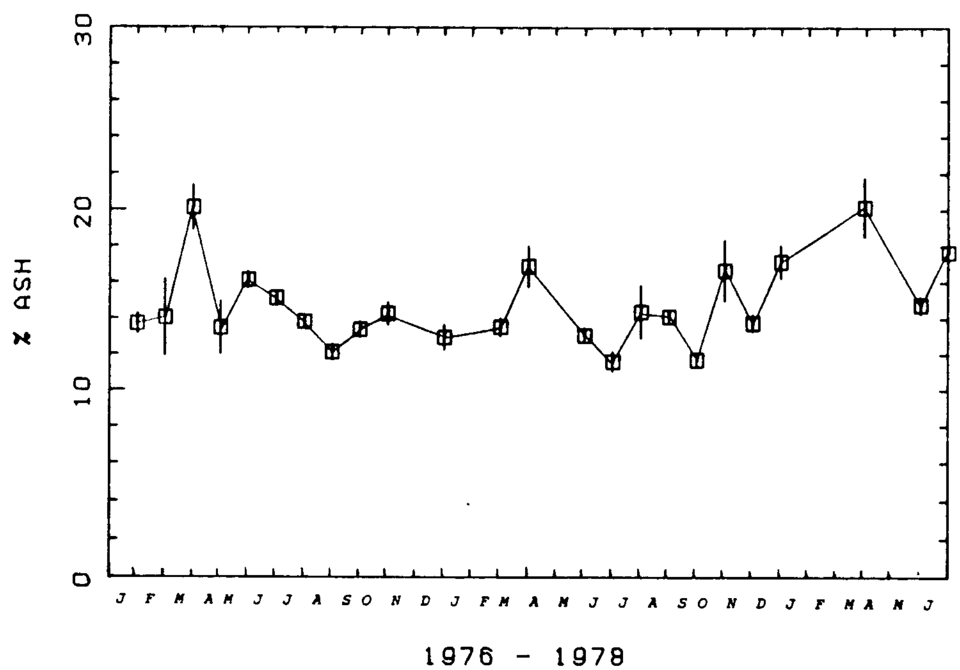
2b. TWENTY-MILE BROOK (1060)



2c. LEE'S MILL STREAM (1100)

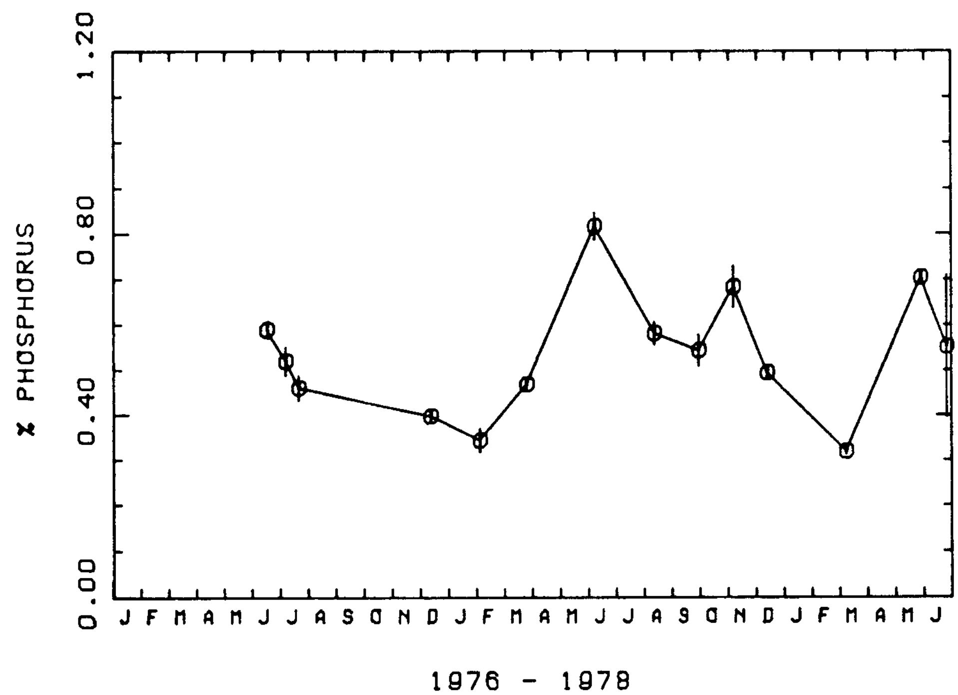


2d. LAZY MEADOW BROOK (1160)

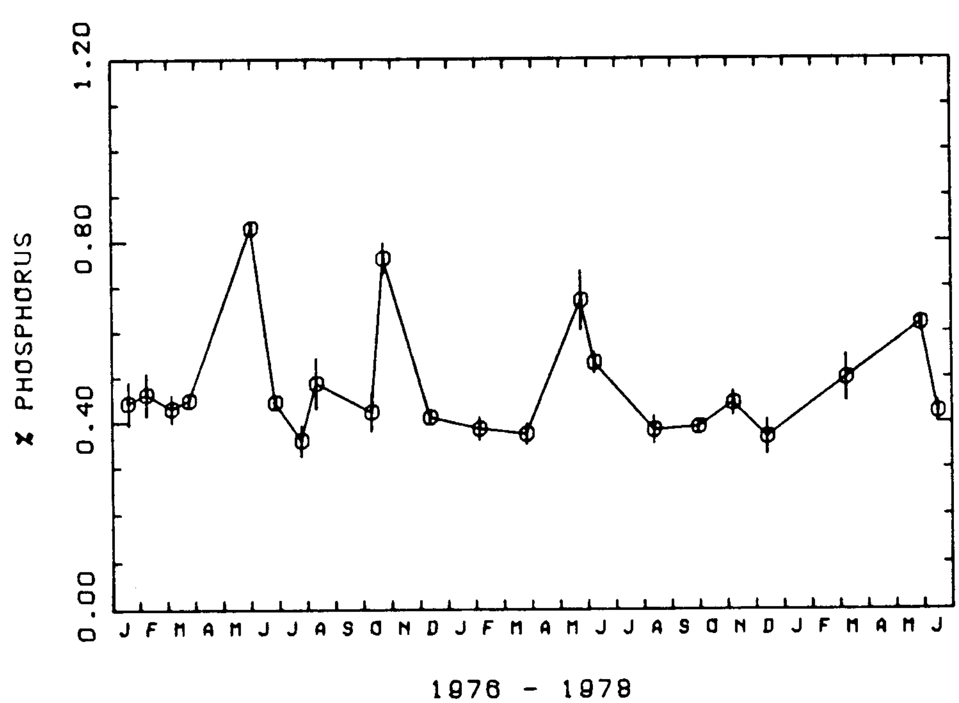


2e. MONTHLY AVERAGE, 9 MAJOR SITES

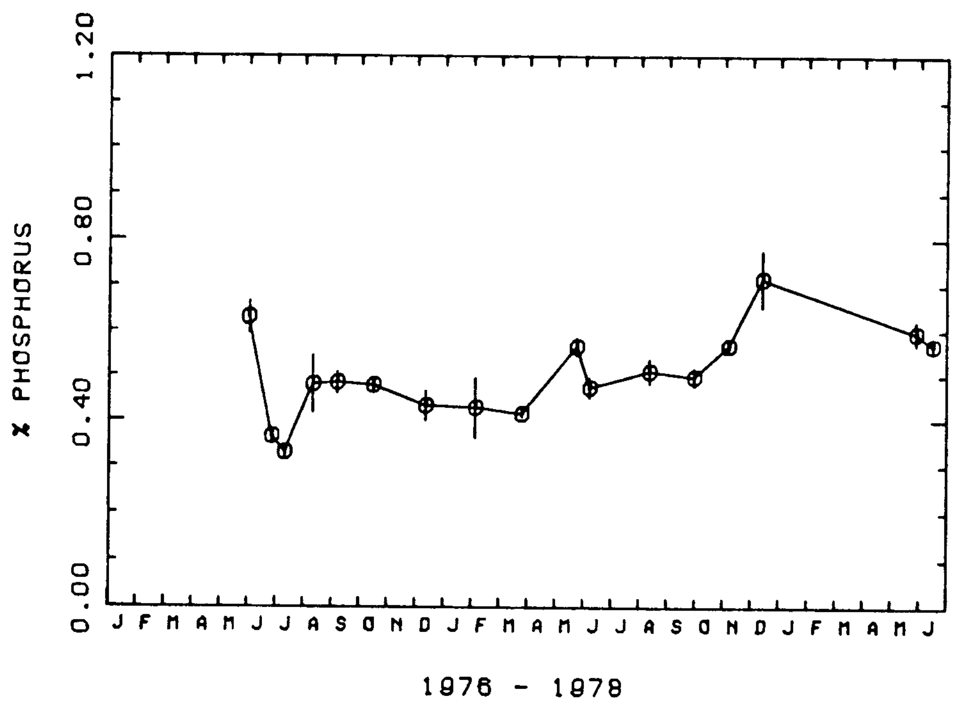
Figs. 2 a-e. Mean concentrations (% dry wt) ash for sampling stations 1030 (a), 1060 (b), 1100 (c), and 1160 (d) and mean monthly values for the nine major sampling locations (e). Vertical bar indicates ± one standard error of the mean.



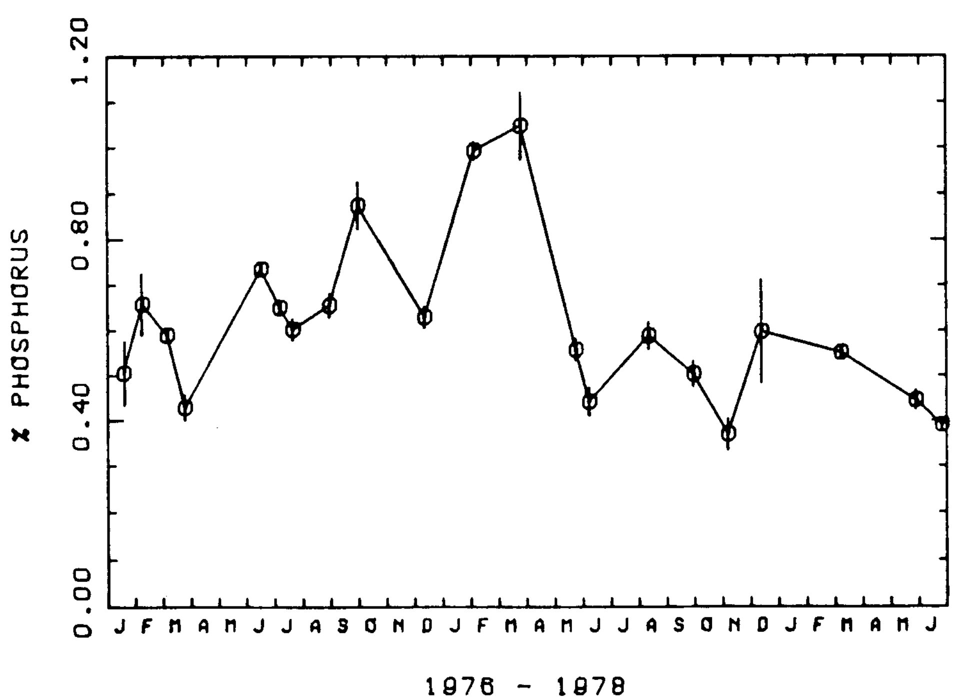
3a, OSTRAND'S MARINA (1030)



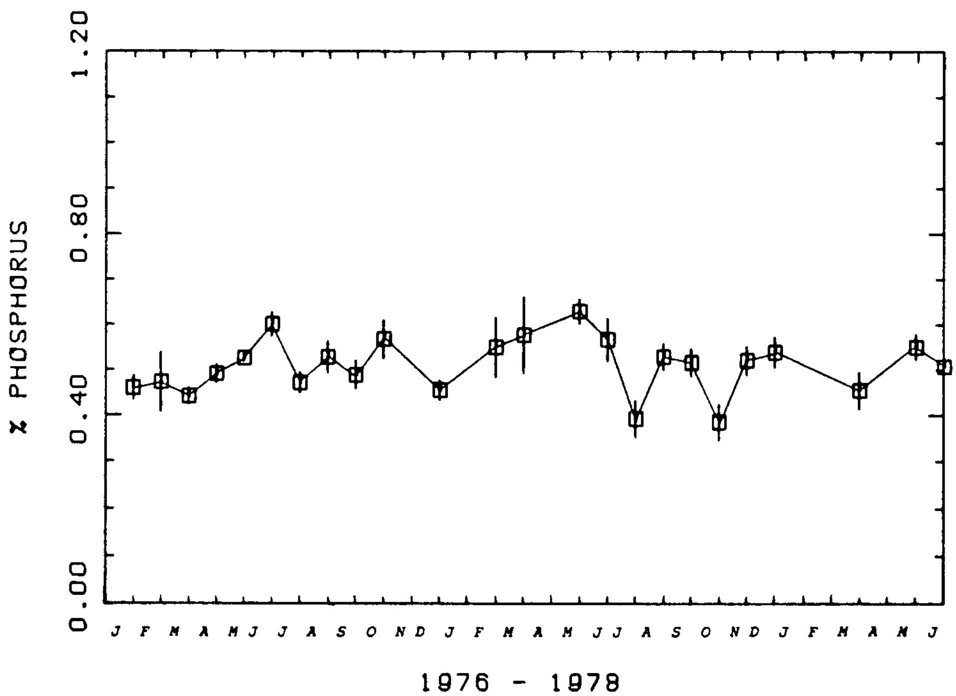
3b. TWENTY-MILE BROOK (1060)



3c. LEE'S MILL STREAM (1100)



3d. LAZY MEADOW BROOK (1160)



3e. MONTHLY AVERAGE, 9 MAJOR SITES

Figs. 3a-e. Mean concentrations (% dry wt) of phosphorus for sampling stations 1030 (a), 1060 (b), 1100 (c), and 1160 (d) and mean monthly values for the nine major sampling locations (e). Vertical bar indicates $\pm$ one standard error of the mean.

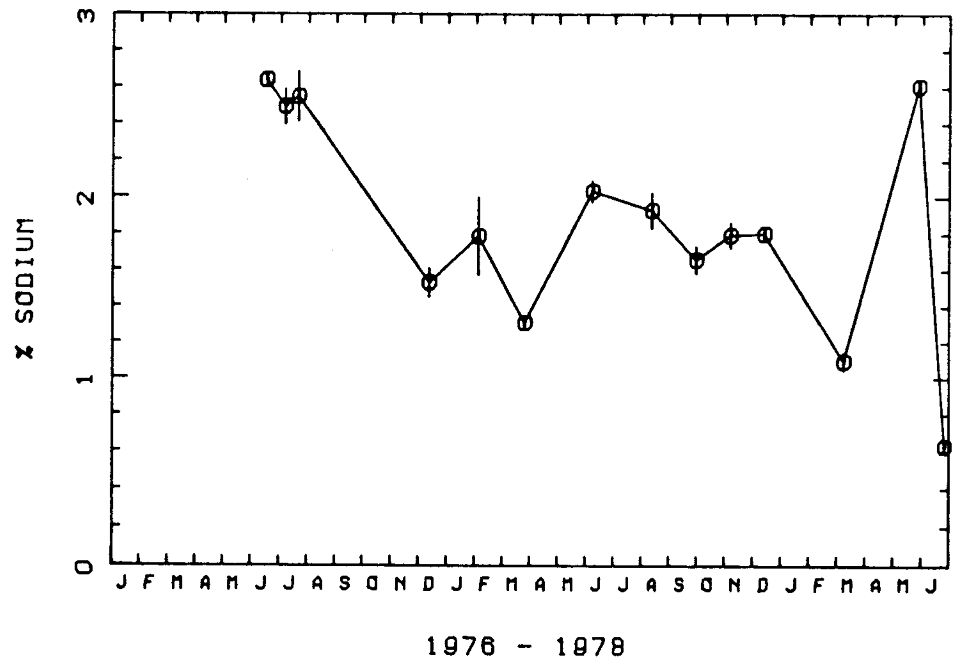
period. Similar patterns were observed during a two-year study of apical and entire-plant tissue level of phosphorus in M. elatinoides (Caines, 1965).

In Lake Winnipesaukee individuals of M. heterophyllum developed emergent floral apices during late June through mid-August under suitable conditions. The distribution of flowering plants was highly variable both within and between stands. The phosphorus content of the emergent floral apices usually exceeded that of the submersed vegetative portions of the plants. Phosphorus demands by emergent floral apex growth, combined with the dilution effect of rapid stem elongation during late spring through mid-summer may explain much of the variability in the apical tissue levels of phosphorus during that time period. The role played by epiphytic algae on the M. heterophyllum leaves and stems during the same period with regard to phosphorus levels is unknown, however growth and accumulation of periphyton occurred throughout the summer at all study sites.

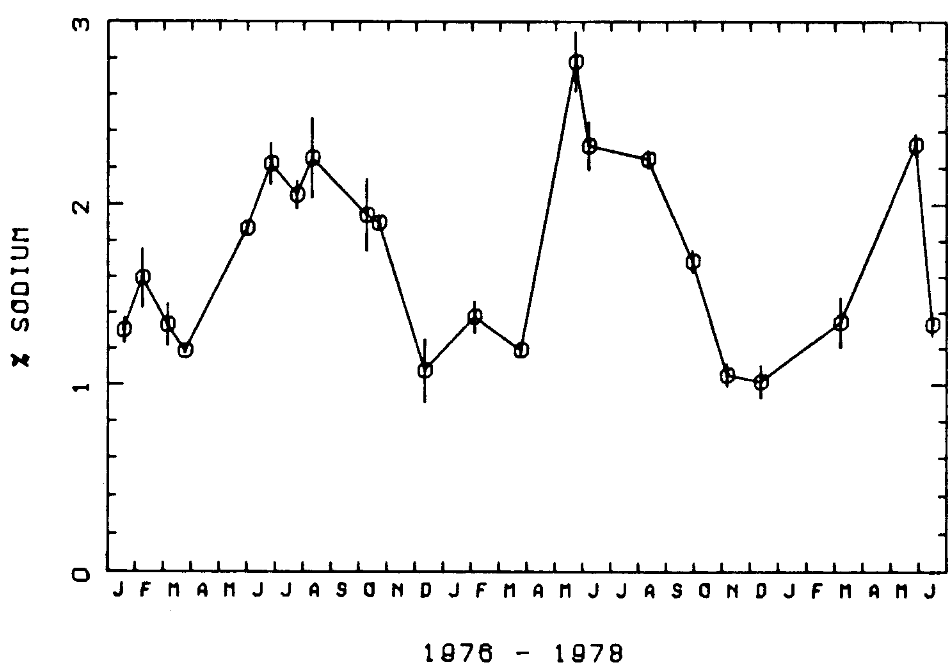
Sodium

Average monthly concentrations of sodium were in the range 0.6 to 2.9% dry weight. Marked seasonal patterns of the element occurred each of the three consecutive years of the study and the trend was similar at most sampling sites. The concentration of sodium in apical tissue during the growing season was higher than during the winter by approximately 60% (Figures 4a-e).

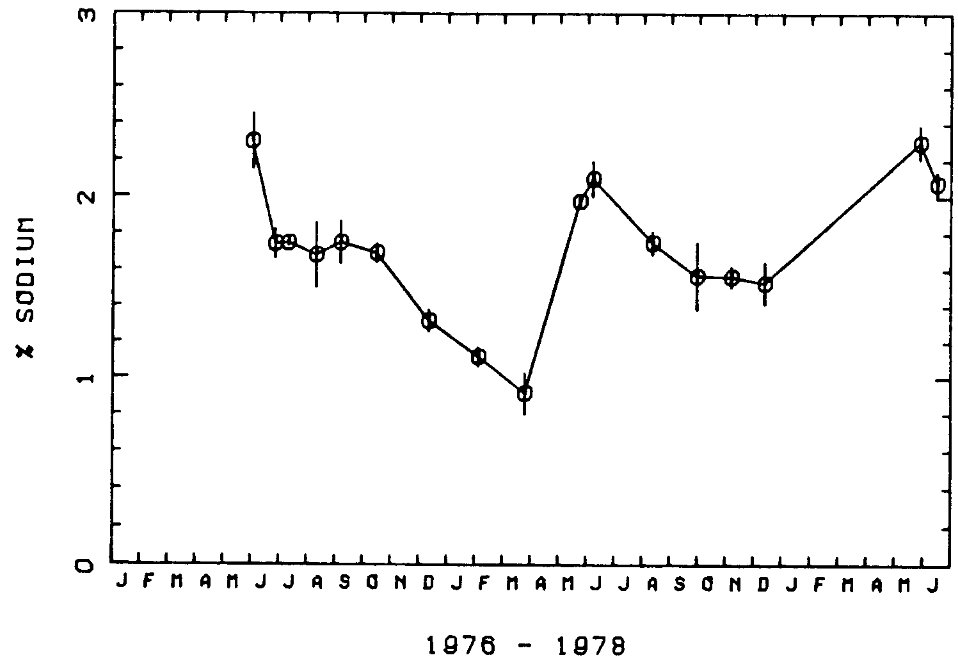
The pronounced seasonal fluctuations may be difficult to interpret, because a requirement for sodium has not been demonstrated for most aquatic plants. However, several emergent aquatic species with the C4 pathway of photosynthesis require sodium as a microelement (Brownell and Crossland, 1972). M. spicatum has a low compensation point for CO_2, and a high temperature optimum for photosynthesis, characteristic of C4 plants, yet no evidence of the C4 pathway has yet been demonstrated (Stanley and Naylor, 1972, 1973). Also, M. heterophyllum lacks the "Krantz anatomy" typical of C4 plants (Hough and Wetzel, 1977).



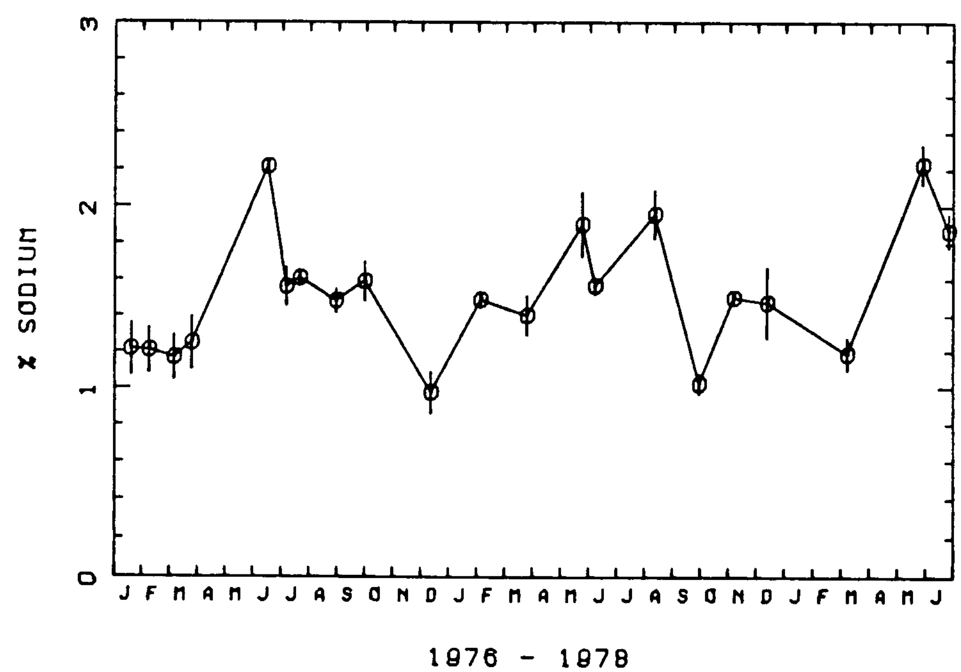
4a. OSTRAND'S MARINA (1030)



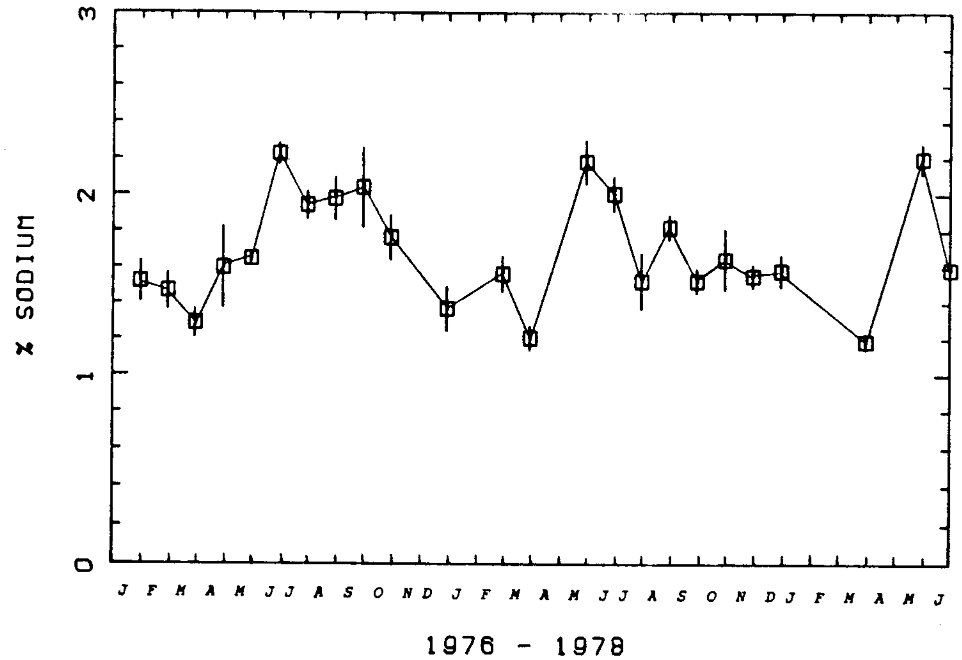
4b. TWENTY-MILE BROOK (1060)



4c. LEE'S MILL STREAM (1100)



4d. LAZY MEADOW BROOK (1160)



4e. MONTHLY AVERAGE, 9 MAJOR SITES

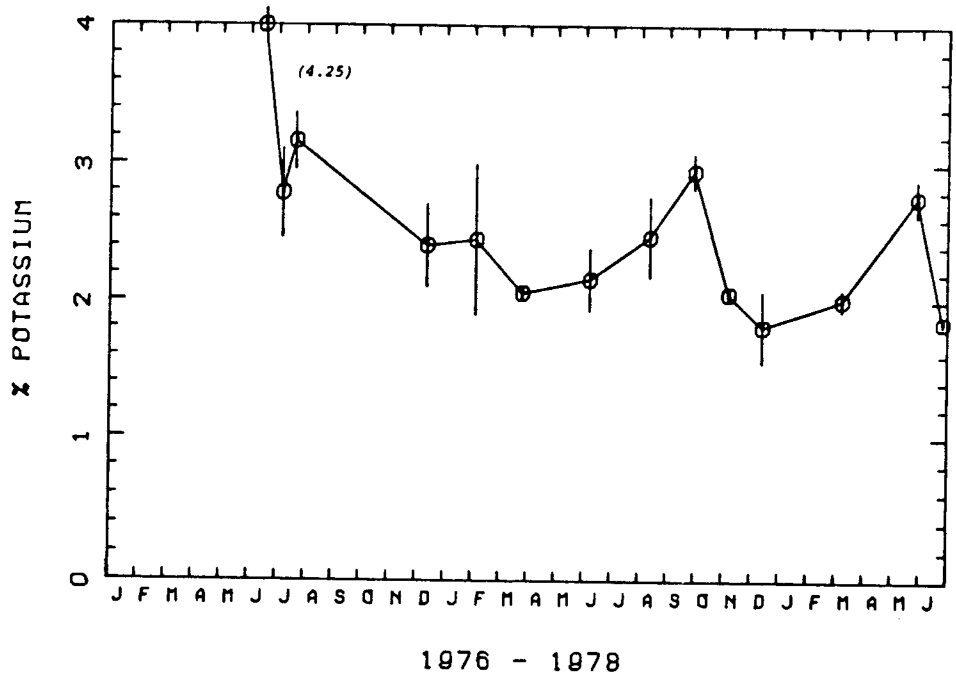
Figs. 4a-e. Mean concentrations (% dry wt) of sodium for sampling stations 1030 (a), 1060 (b), 1100 (c), and 1160 (d) and mean monthly values for the nine major sampling locations (e). Vertical bar indicates $\pm$ one standard error of the mean.

Sodium in the tissue of *Najas* sp. was reported to be positively correlated with the sodium level of the water (Martin, Bradford and Kennedy, 1969). Samples of *M. spicatum* collected along a salt gradient in estuaries of Chesapeake Bay had a high correlation of the location of the sample and the sodium level in the tissue (Anderson, Brown and Rappleye, 1966). During the past three decades the sodium level of Lake Winnipesaukee has increased significantly due to the increased use of road-salt during the winter (Hall, 1975). Lakewater in New Hampshire remote from highways have sodium levels less than 1 $mg\ell^{-1}$, while levels of sodium in Lake Winnipesaukee exceeded 8 $mg\ell^{-1}$ in 1975 (NHWSPCC, 1975). The possible role that sodium has played in the recent proliferation of water milfoil into the lake is unknown. Possibly the sodium acts as a growth stimulant, similar to the measured increase in rates of carbon fixation and secretion of organic matter from *Najas flexis* after addition of sodium, observed by Wetzel (1969).

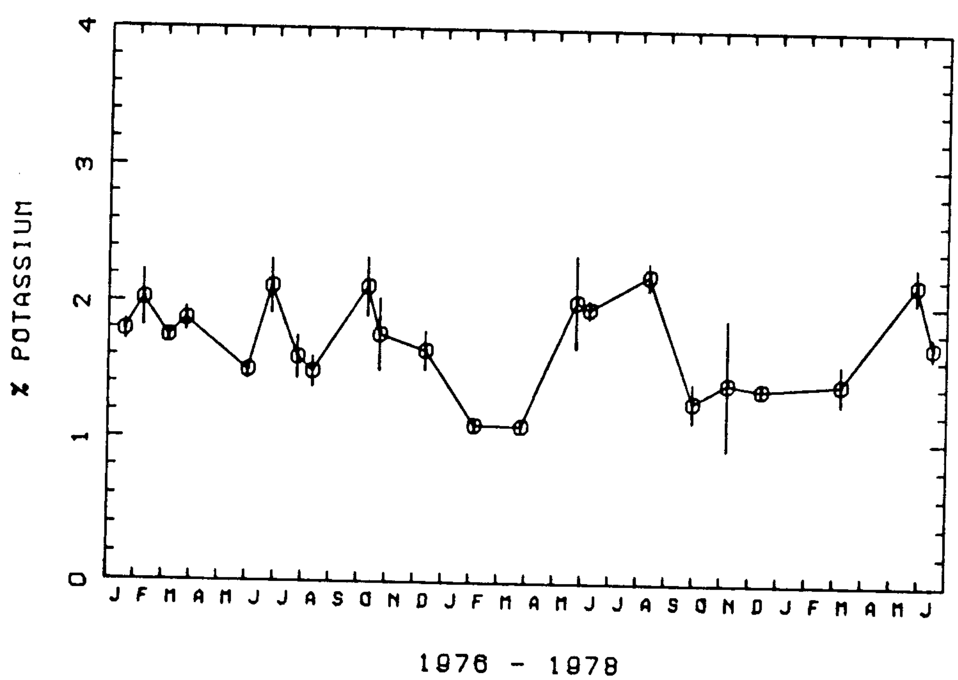
The role of the sediments in the availability of sodium to aquatic macrophytes is poorly understood. Martin, Bradford and Kennedy (1969) found a linear decrease in the rate of sodium uptake by *Najas* when sediments were diluted with nutrient-free sand. We observed considerably lower sodium levels in the roots and emergent floral apices of *M. heterophyllum* than in the submergent stem and apex tissue. If sodium was being obtained mainly from sediments, as we believe, then a rapid translocation to the stem and apices was occurring.

Potassium

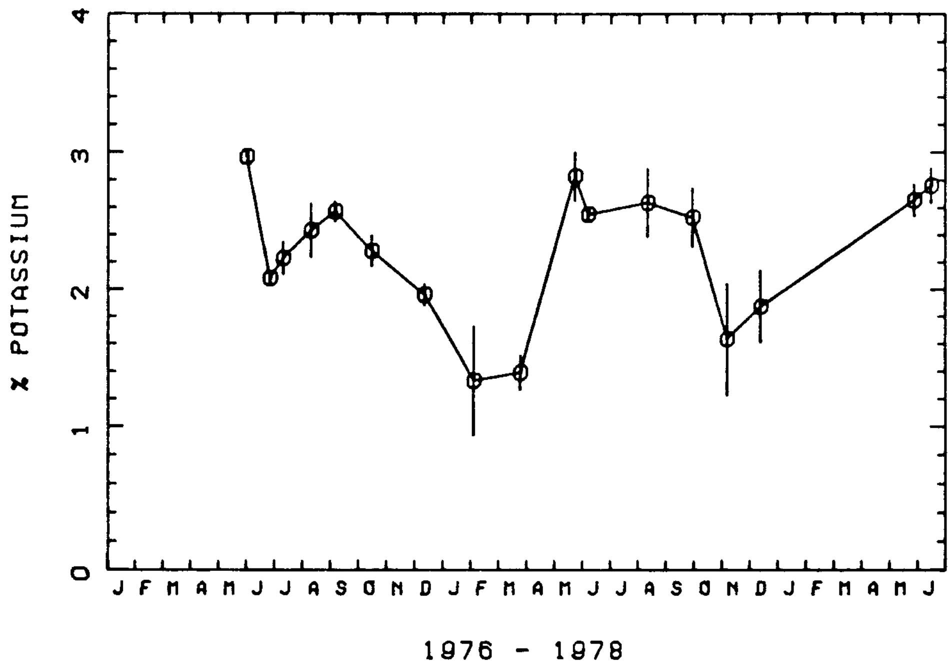
The levels of potassium in the apices of *M. heterophyllum* were similar and varied through the year in the same way as those of sodium (Figures 5a-e). Mean monthly values of potassium in the apices at the nine major sampling stations were in the range of 1.1 to 4.35% dry weight, and the K:Na ratio was generally 1.21:1. A similar or higher ratio is common in most plant tissue. Generally the level of potassium in the apical tissue was less than 2.0% dry weight during the winter through late spring, but often exceeded



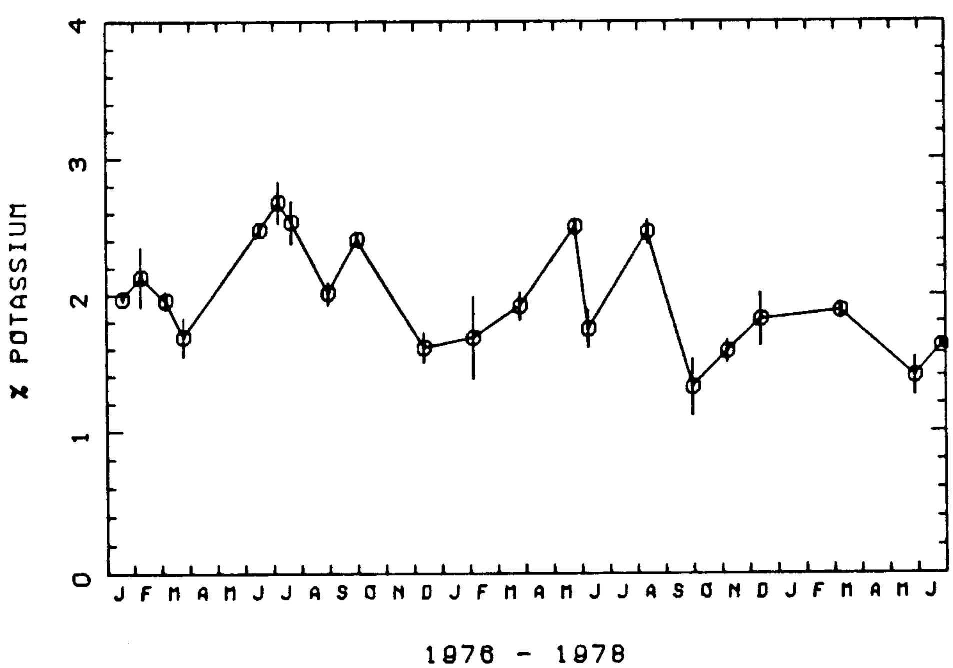
5a. OSTRAND'S MARINA (1030)



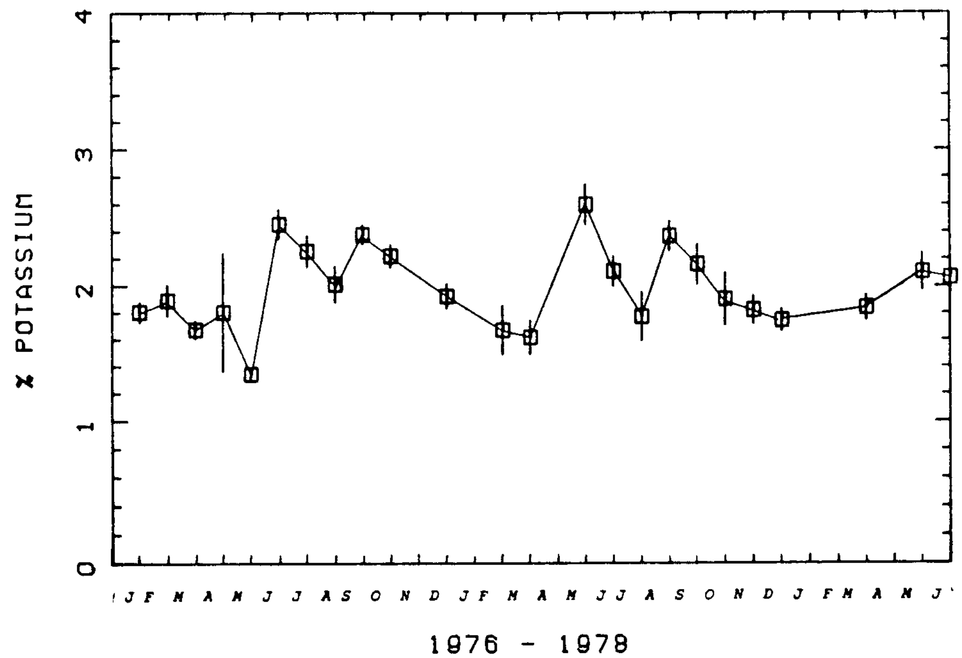
5b. TWENTY-MILE BROOK (1060)



5c. LEE'S MILL STREAM (1100)



5d. LAZY MEADOW BROOK (1160)



5e. MONTHLY AVERAGE, 9 MAJOR SITES

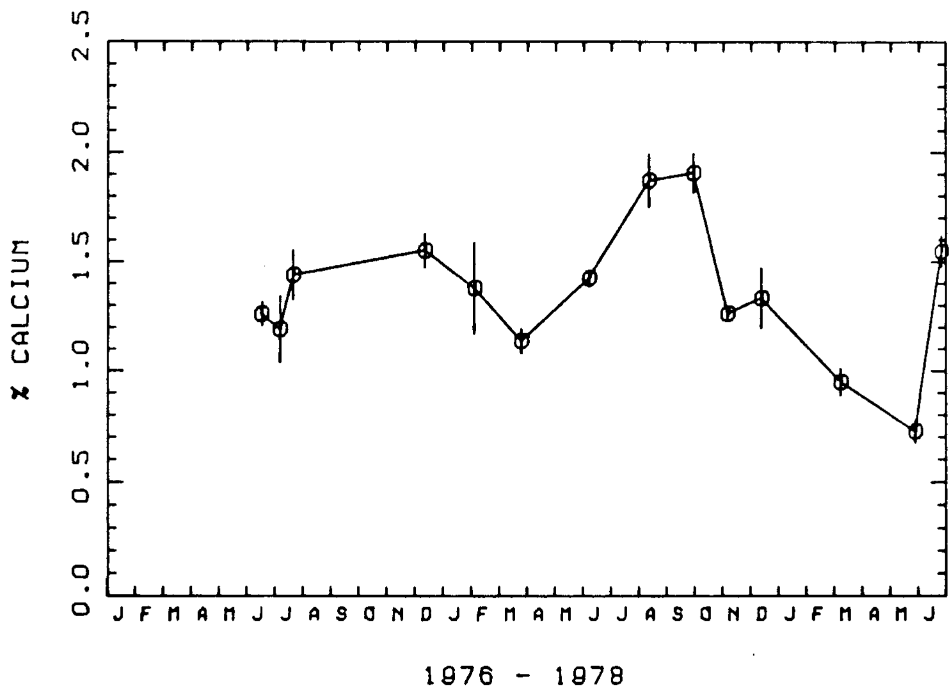
Figs. 5a-e. Mean concentrations (% dry wt) of potassium for sampling stations 1030 (a), 1060 (b), 1100 (c), and 1160 (d) and mean monthly values for the nine major sampling locations (e). Vertical bar indicates ± one standard error of the mean.

2.6% during the spring to mid-summer.

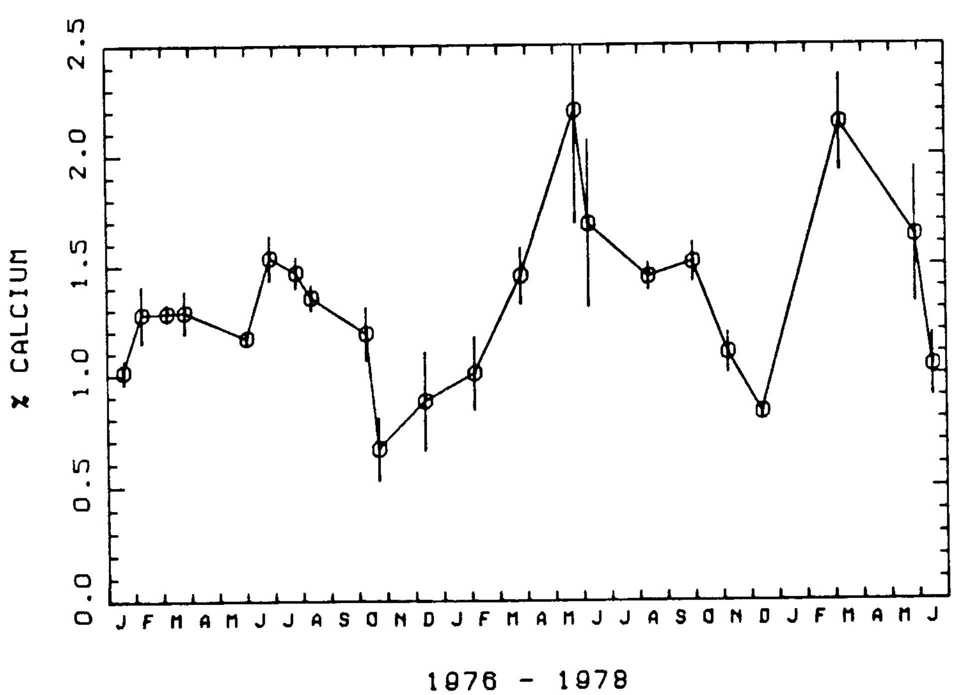
Martin, Bradford and Kennedy (1969) demonstrated that potassium was absorbed by *Najas* both from the lakewater and from the sediments, although no correlation was found between apical level of potassium and levels of the cation in the surrounding water. Anderson, Brown and Rappleye (1966) suggested on the basis of slight variations in tissue levels of potassium between fresh-water and brackish sites that *M. spicatum* is able to regulate the rate of potassium uptake independent of the levels of the element in the surrounding water. Concentration gradients of potassium within *M. heterophyllum* from root to apex differ from those of sodium during the growing season, with the submergent stems > roots ≥ apices > floral apices. The higher levels in the lower stem and roots may be the result of concentration in those tissues during the growing season. Low levels of potassium in the apices relative to the stems have also been measured in *M. spicatum* (Livermore et al., 1975) and in *Elodea canadensis* (Rawlence and Whitton, 1977).

Calcium

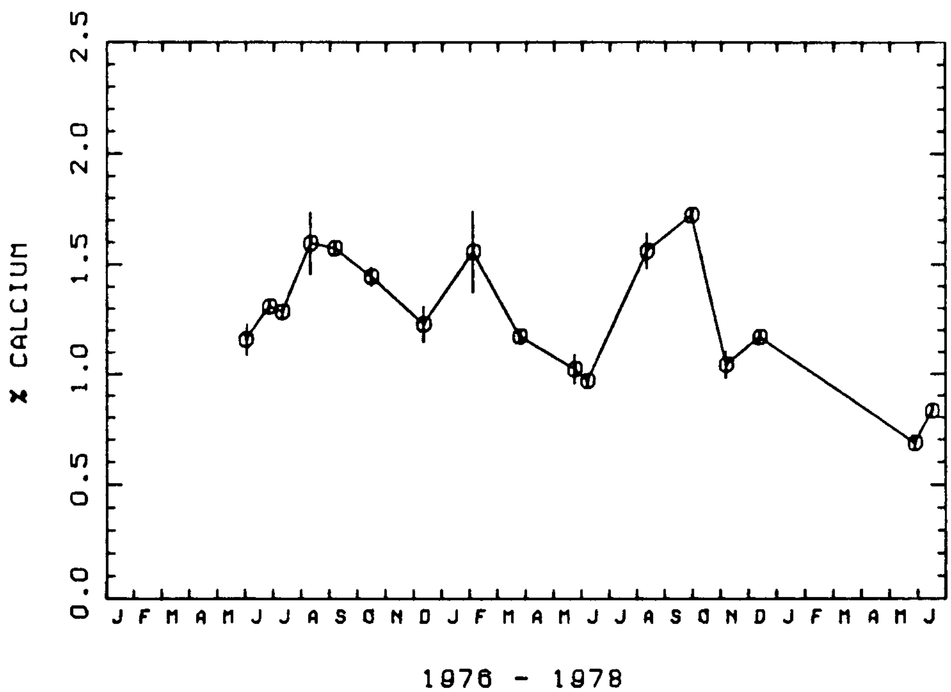
Mean monthly levels of calcium in the apical tissue of *M. heterophyllum* were in the range of 0.5 to 2.2% dry weight at the nine major sampling sites. The levels varied markedly between sites on given dates (Figures 6a-e). Studies of calcium levels in the tissue of submersed macrophytes have been conducted mainly in hard-water lakes where the seasonal trends have been masked by a precipitation of marl on the shoots. At our study sites, no evidence of marl precipitation on the exterior of either submersed or emergent apices was found, and the lakewater is extremely soft with a calcium level of less than 5 $mg\ell^{-1}$. It is unlikely that any of the observed high levels of calcium in the submersed apices was a result of marl precipitation on the outside of the epidermis. The role of sediments in supplying calcium is not understood, however, we measured this cation's concentrations to be lowest in the roots and highest in the floral apices of *M. heterophyllum*. The lack of marked seasonal trends in the apical level of calcium may be explained in part by



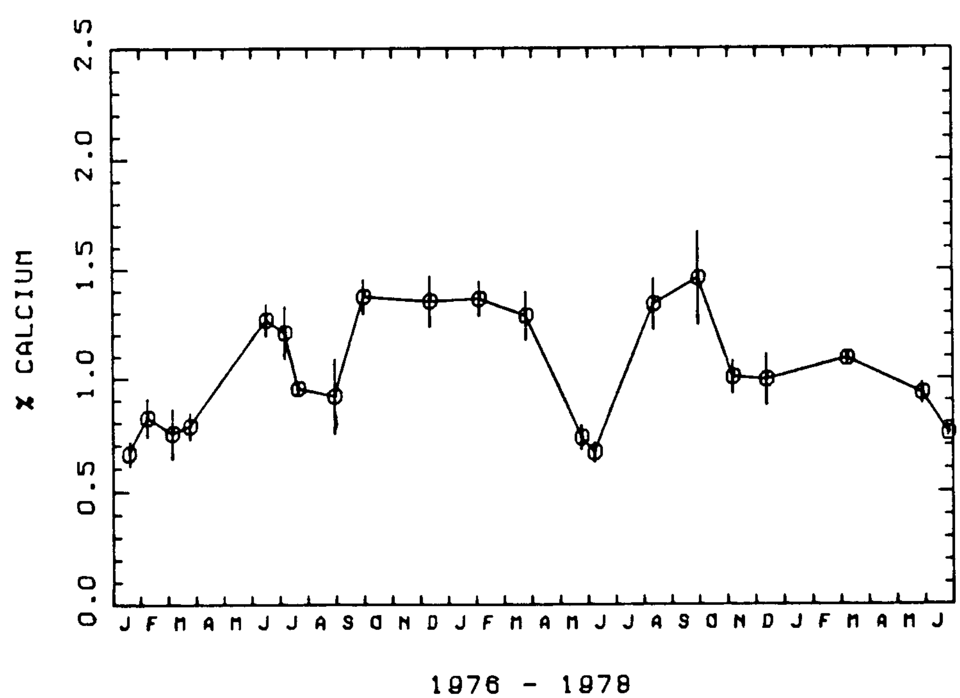
6a. OSTRAND'S MARINA (1030)



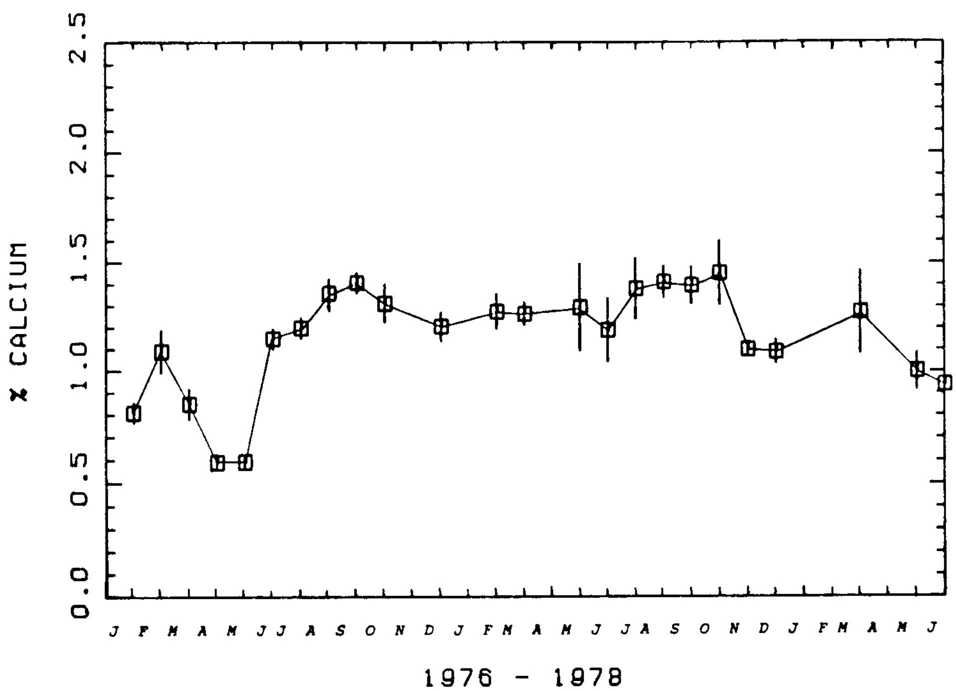
6b. TWENTY-MILE BROOK (1060)



6c. LEE'S MILL STREAM (1100)



6d. LAZY MEADOW BROOK (1160)



6e. MONTHLY AVERAGE, 9 MAJOR SITES

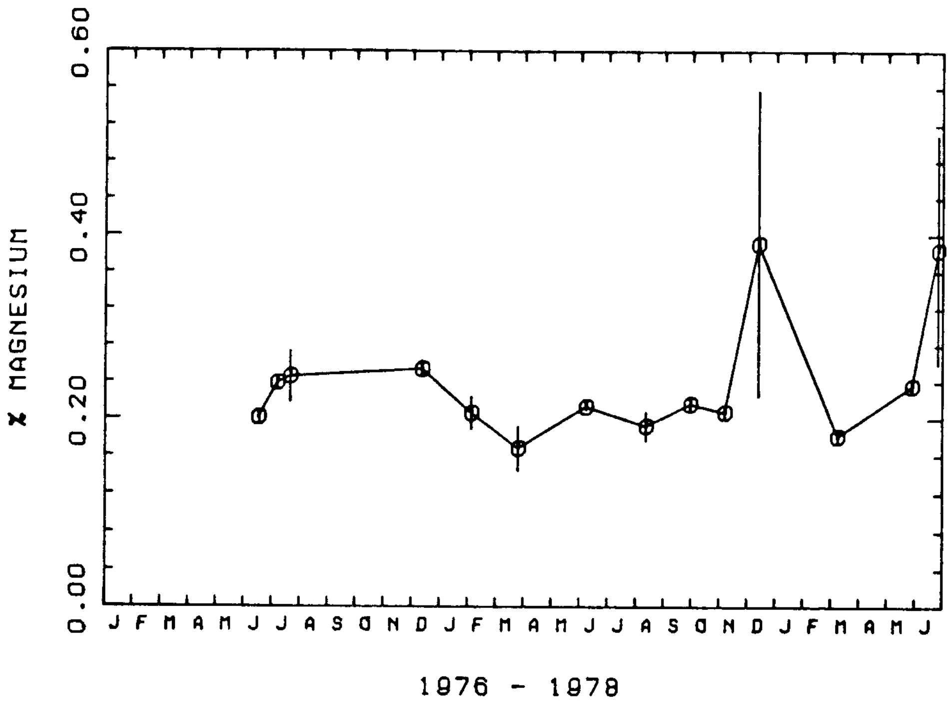
Figs. 6a-e. Mean concentrations (% dry wt) of calcium for sampling stations 1030 (a), 1060 (b), 1100 (c), and 1160 (d) and mean monthly values for the nine major sampling locations (e). Vertical bar indicates ± one standard error of the mean.

the presence or absence of the floral stem. We postulate that the high levels in the emergent apices could be due to a high calcium requirement, because the element is a major constituent of the middle lamella as calcium pectate (Nason and McElroy, 1963). The emergent stem requires more structural support than the submersed portions, to maintain an upright position during the period of flowering. A second possibility is that calcium is carried apically within the transpirational stream to the emergent apices. If translocation of calcium is negligible in plant tissue (Nason and McElroy, 1963), calcium would either be secreted or accumulated in the emergent tissue.

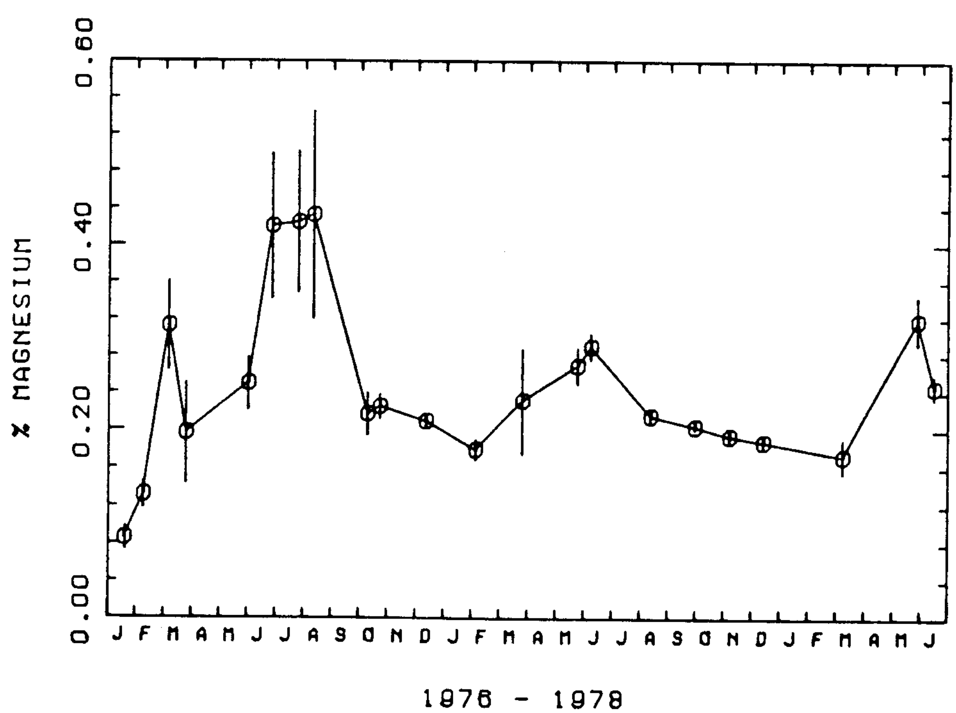
Magnesium

Mean monthly magnesium levels were in the range of 0.09 to 0.43% dry weight. No seasonal pattern was detected (Figures 7a-e), and the time of occurrence of maximum concentrations was quite variable (Figures 7a-b). Indistinct variations in magnesium levels were also observed in *Elodea canadensis* and *Ceratophyllum demersum* (Best, 1977). Unlike most bivalent cations, magnesium is appreciably mobile in the phloem (Clarkson, 1974). Magnesium is a constituent of the chlorophyll molecule and generally is associated with physiologically young cells, rapid growth and active mitosis. With increasing plant maturity, magnesium can be withdrawn from vegetative parts and used in seed formation (Nason and McElroy, 1963).

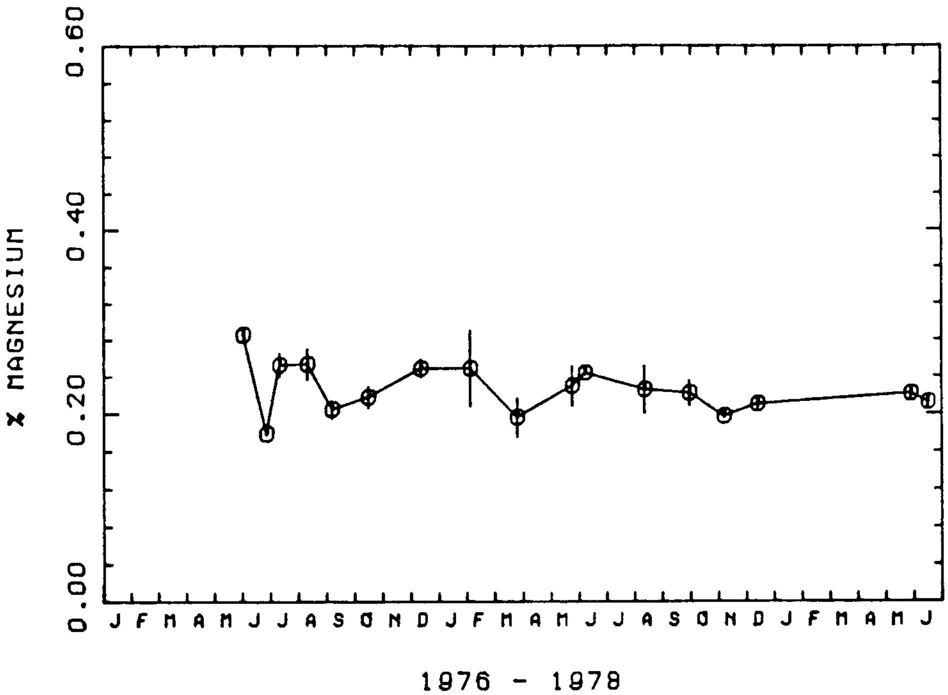
Decreasing magnesium concentrations in water had little effect on magnesium uptake in *Najas* sp. (Martin, Bradford and Kennedy, 1969) or *M. spicatum* (Anderson, Brown and Rappleye, 1966). Martin, et al., did find a decrease in magnesium uptake when sediments were diluted with inert sands. During the summer we measured a two- to threefold increase in magnesium concentration from the roots to the apex, suggesting rapid upward translocation from the sediments. If magnesium is rapidly shuttled to zones of active cell division, the physiological state of the apex would strongly influence apical magnesium content.



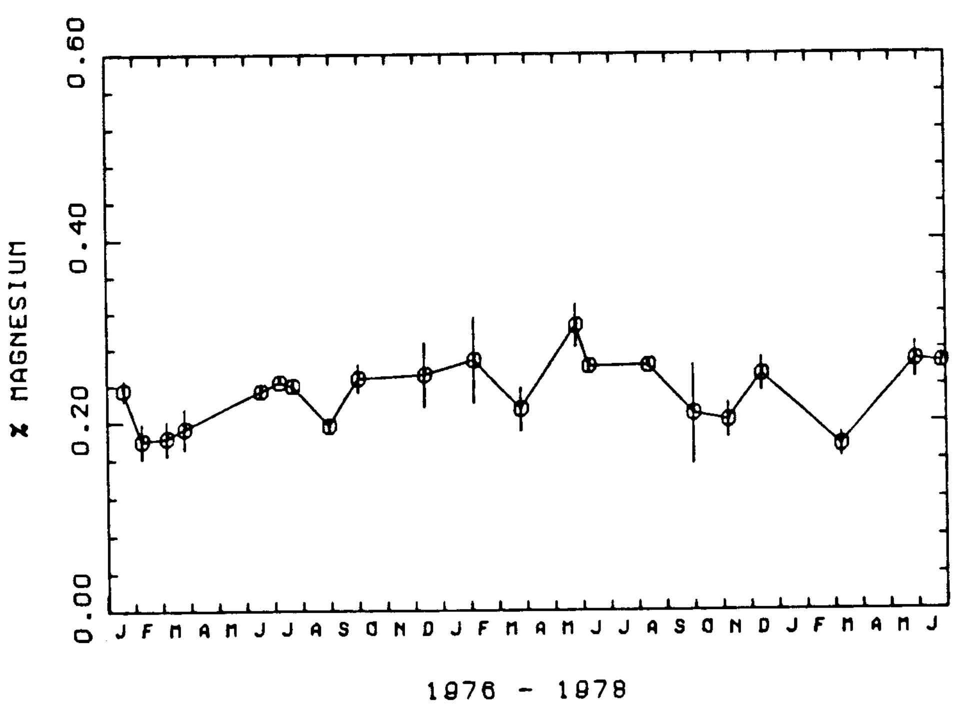
7a. OSTRAND'S MARINA (1030)



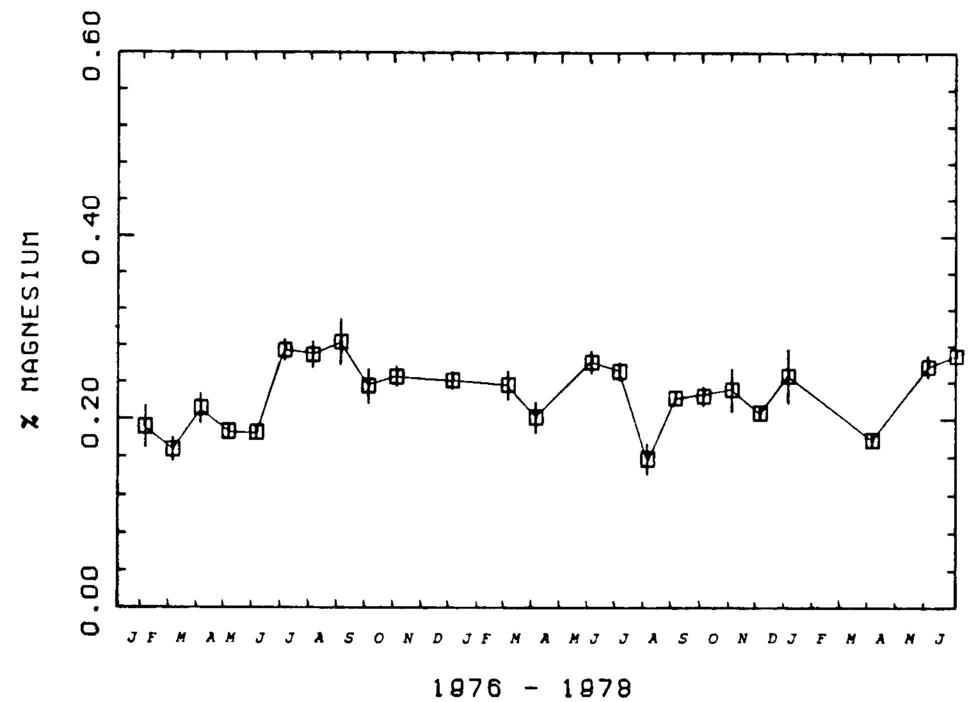
7b. TWENTY-MILE BROOK (1060)



7c. LEE'S MILL STREAM (1100)



7d. LAZY MEADOW BROOK (1160)



7e. MONTHLY AVERAGE, 9 MAJOR SITES

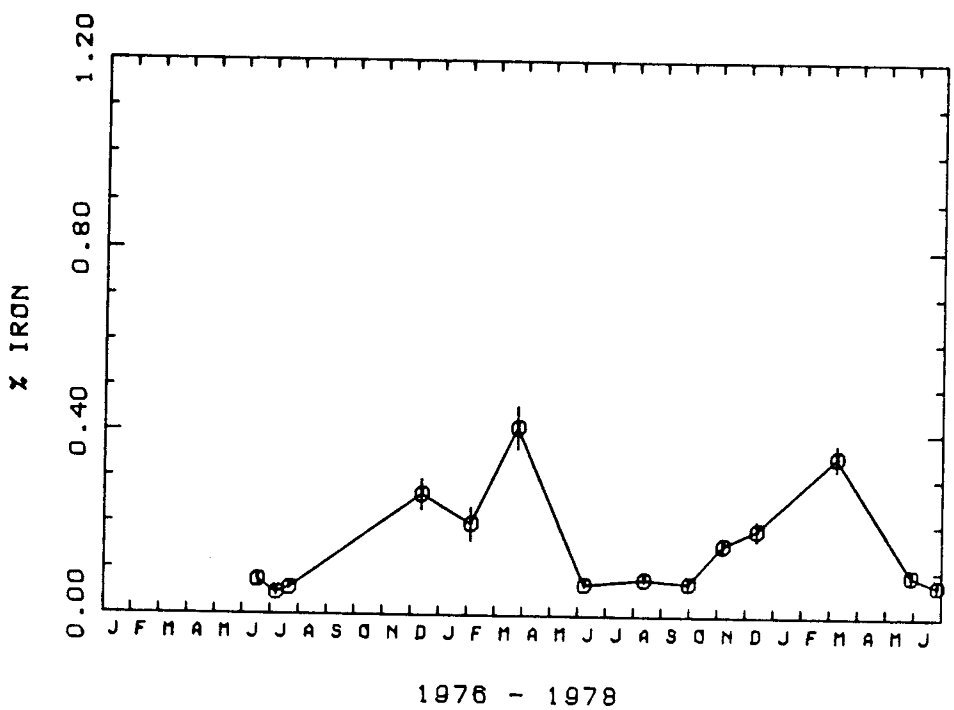
Figs. 7a-e. Mean concentrations (% dry wt) of magnesium for sampling stations 1030 (a), 1060 (b), 1100 (c), and 1160 (d) and mean monthly values for the nine major sampling locations (e). Vertical bar indicates ± one standard error of the mean.

Iron

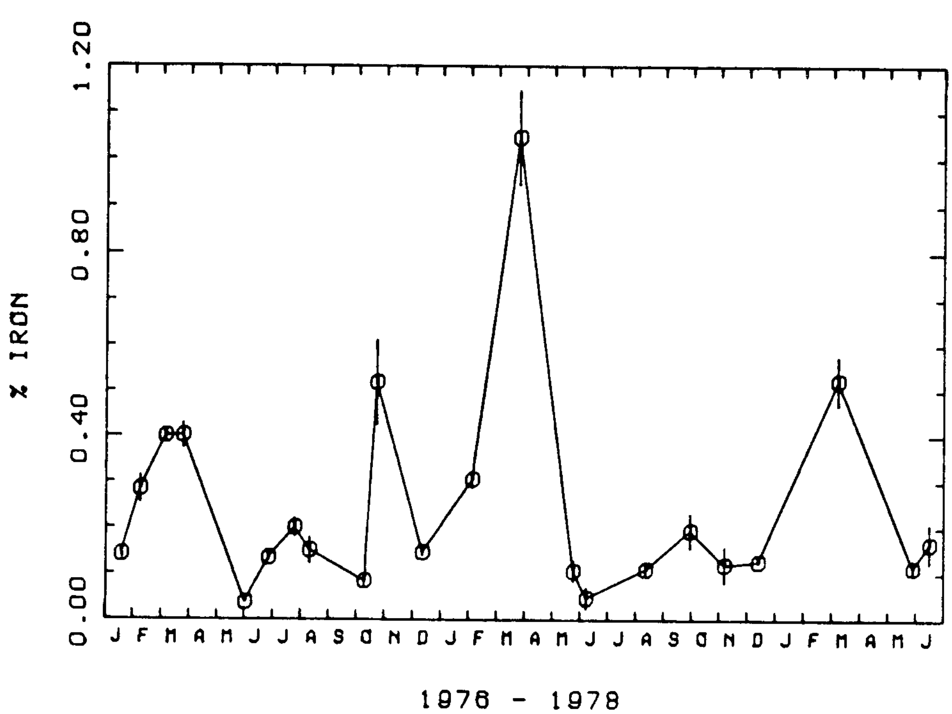
Iron is associated with numerous critical enzymes - peroxidase, catalase, cytochrome oxidase and others, and with the photosynthetic pigment system. Iron is the most abundant heavy metal in the earth's crust, and its moderately high concentration in New Hampshire's waters is typical, because of the regional geology, acidic waters, and presence of organic chelating agents. In our study, the range for mean monthly iron concentrations in the apical tissue was 0.03 to 1.20% dry weight.

Hutchinson (1975) and Riemer and Toth (1969) concluded that it is difficult to make generalizations for iron and manganese concentrations in submersed aquatic macrophytes, because of the high variability encountered. Our results show definite temporal and spatial patterns (Figures 8a-e), which account for much of the variability. Minimum values below 0.15% dry weight during the ice-free season (May - December) were followed by a two- to six-fold increase during the ice covered season (December - April). Tributary sample sites exceeded non-tributary sites in apical iron content (paired t-test; $n = 3.39$, $df = 16$, $0.01 > p > 0.001$) and the respective winter maxima in iron were much more pronounced (Figures 8b, 8d). Proximity to allochthonous input sources and seasonal changes in iron content have also been measured in M. spicatum (Carpenter and Adams, 1977), Ceratophyllum demersum and Elodea canadensis (Best, 1977).

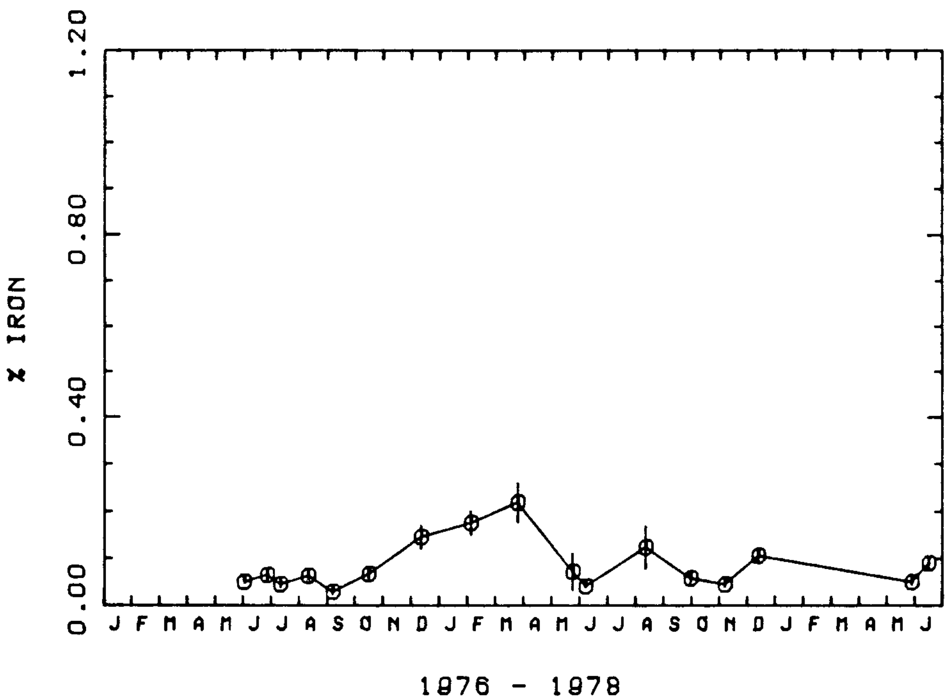
Throughout the year, the low redox potential of the sediments favor iron (Fe^{++}) availability to the roots. Gentner (1977) and DeMarte and Hartman (1974), using the radioisotope $^{59}Fe^{3+}$ with Vallisneria spiralis and Myriophyllum exalbescens respectively, observed that the majority of iron is translocated from the roots to the shoots. We measured considerably higher root than shoot concentrations of iron. The high iron levels at tributary sites could be related to increased rates of particulate matter loss from the watershed during periods of maximal discharge, which occur in March. Iron, unlike most chemicals, is transported into lakes primarily as particulate matter, rather than in the dissolved form



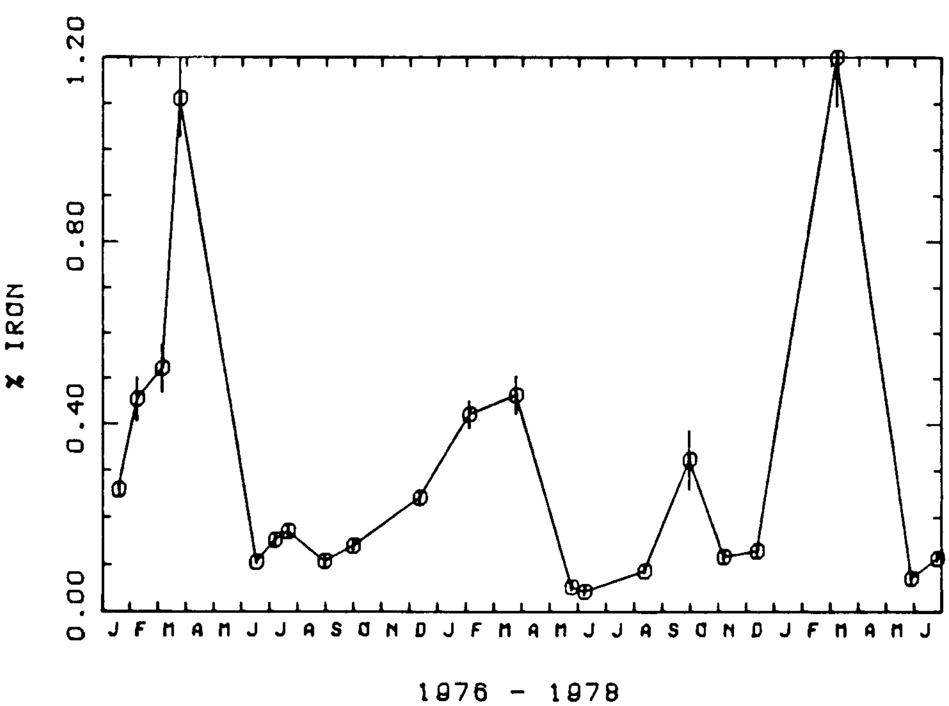
8a. OSTRAND' MARINA (1030)



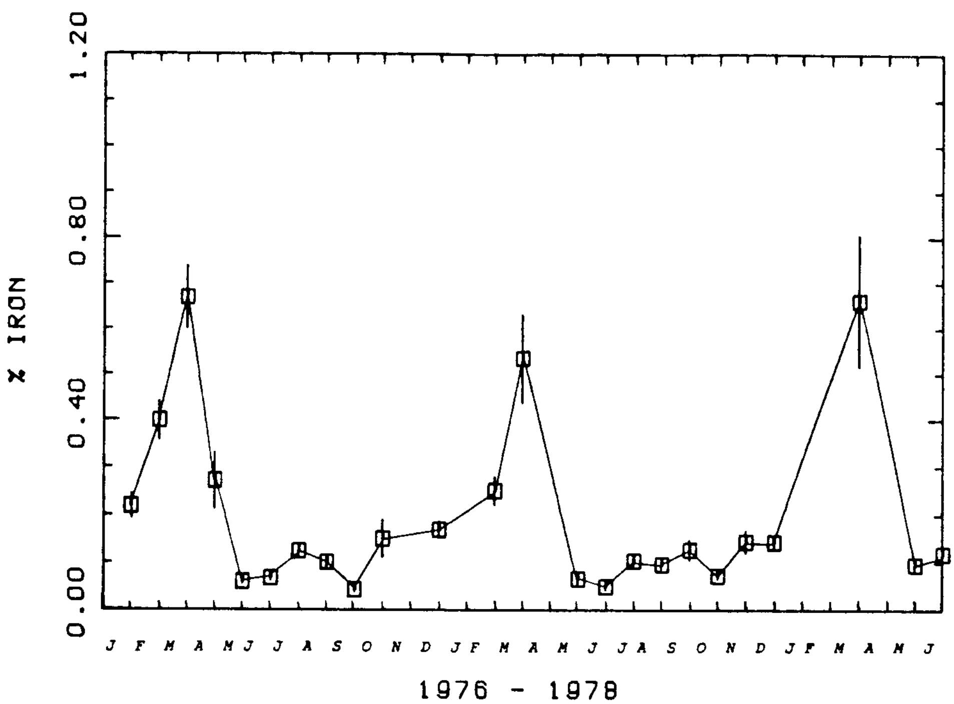
8b. TWENTY-MILE BROOK (1060)



8c. LEE'S MILL STREAM (1100)



8d. LAZY MEADOW BROOK (1160)



8e. MONTHLY AVERAGE, 9 MAJOR SITES

Figs. 8a-e. Mean concentrations (% dry wt) of iron for sampling stations 1030 (a), 1060 (b), 1100 (c), and 1160 (d) and mean monthly values for the nine major sampling locations (e). Vertical bar indicates $\pm$ one standard error of the mean.

(Borman, Likens and Eaton, 1969). Possibly, the prostrate habit of the plant during March with the apices often in close proximation to the sediments favors the assimilation of iron rich particles being transported through the tributary sites during late winter and early spring. Uptake of chelated iron increases in detached apical sections of *Hydrilla verticillata*, with increasing levels of Fe-EDTA nutrient solution (Basiouny, Garrard and Haller, 1977). Whether the iron is adsorbed or absorbed has not been determined.

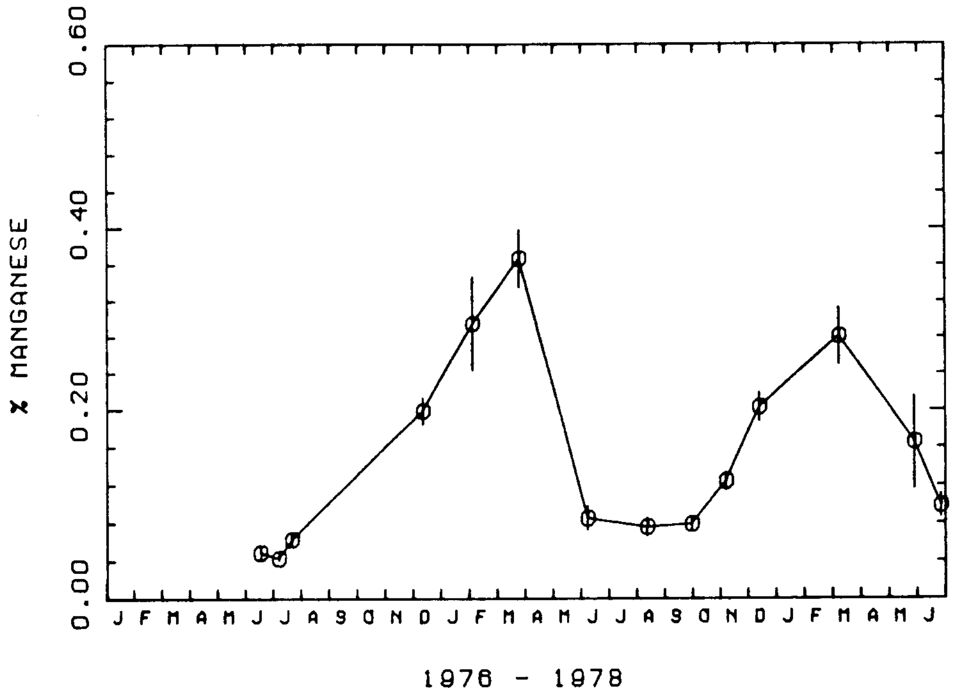
Manganese

Seasonal variations in the level of manganese in apical tissue of *M. heterophyllum* are similar to those of iron. Maximal concentrations in the submersed apices (0.3 to 0.6% dry weight) occurred during the winter/early spring season, followed by a marked decline to 0.02 to 0.12% dry weight during the summer (Figures 9a-e). Patterns found with whole stem analysis of *C. demersum* and *E. canadensis* were similar (Best, 1977). Although not significantly different, tissue manganese levels in submersed apices at tributary sites in our study exceeded those at non-tributary sites and the seasonal maxima were more pronounced (Figures 9b, 9d). The range of mean monthly manganese concentrations was 0.01 to 0.64% dry weight.

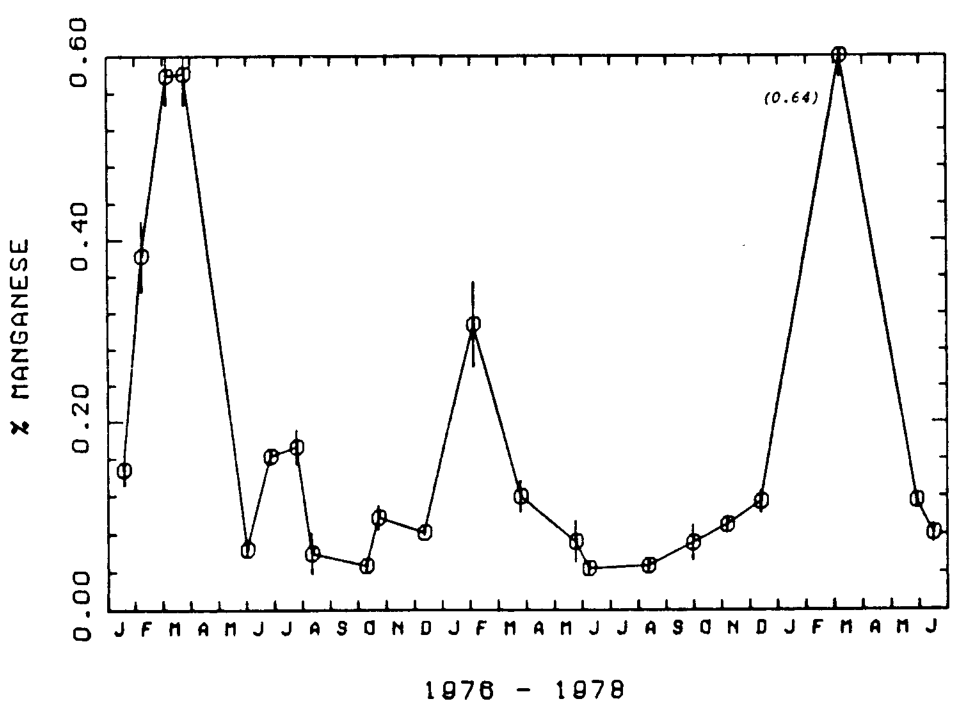
Unlike iron, manganese concentrations were considerably lower in the roots than in the stem. Why apical iron and manganese concentrations had similar temporal patterns is unknown. In contrast, results of culture experiments with detached *Hydrilla* apices, suggested the presence of a competitive relationship between iron and manganese (Basiouny, Garrard, and Haller, 1977). Manganese is considered essential in respiration and nitrogen metabolism as an enzyme activator; deficiency studies suggest a direct role for manganese in photosynthesis (Nason and McElroy, 1963).

Zinc

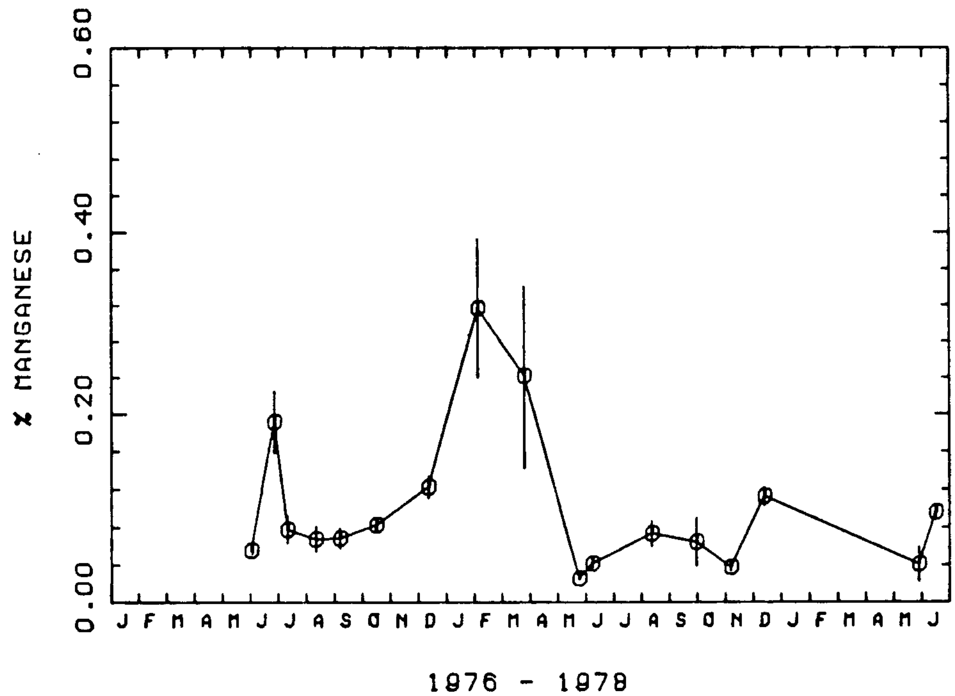
Average zinc concentrations reported to occur in *Myriophyllum* spp. are quite variable. Carpenter and Adams (1977) recorded typical summer shoot concentrations of 20 $ug.g^{-1}$ in *M. spicatum*.



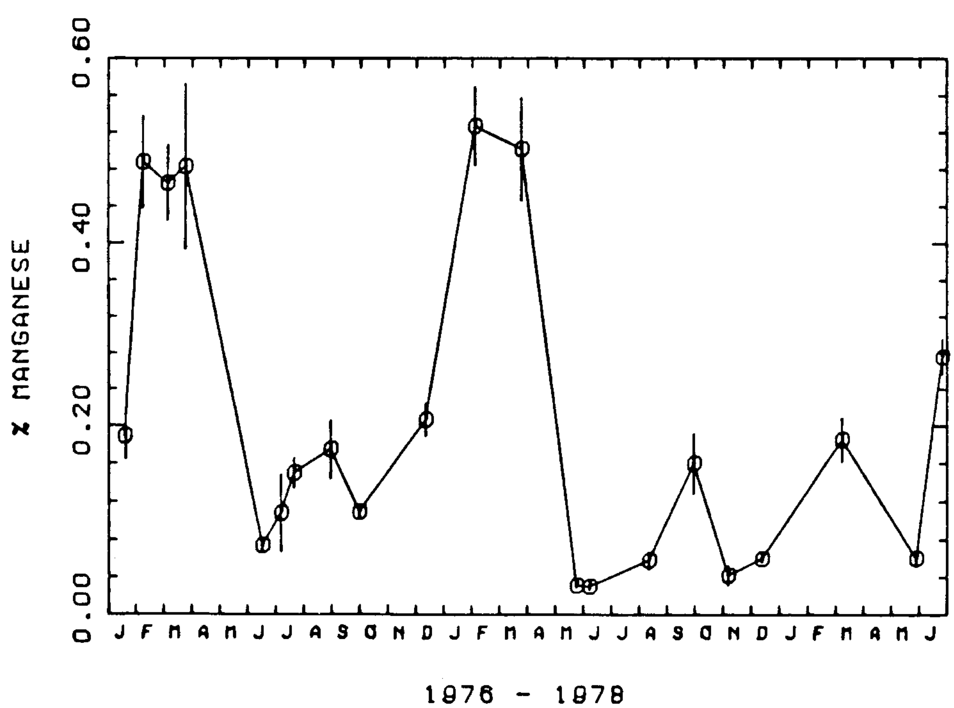
9a.- OSTRAND'S MARINA (1030)



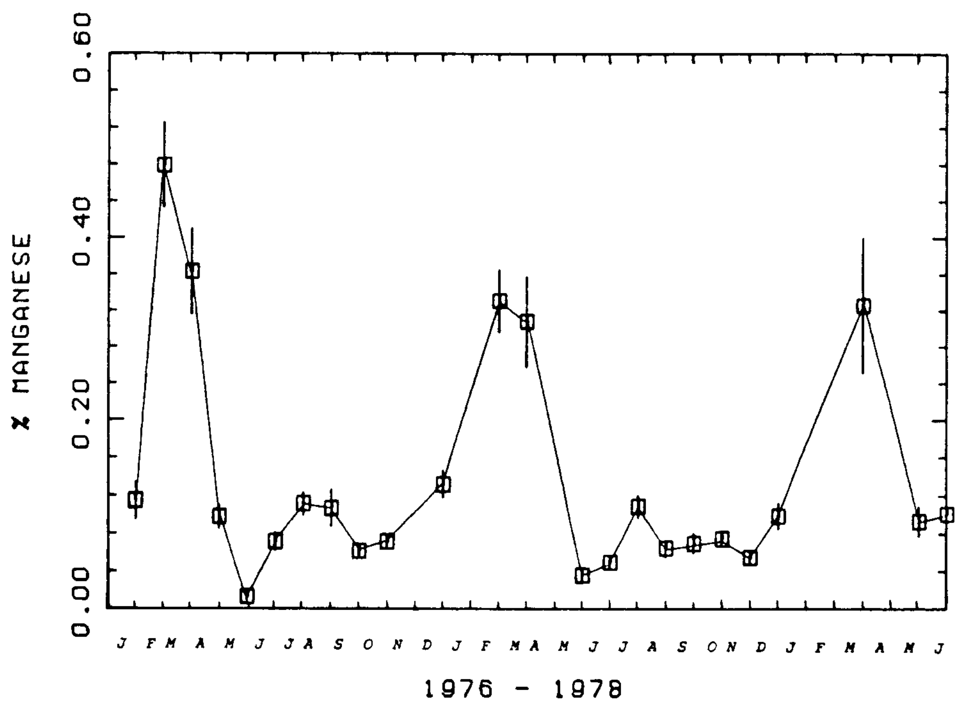
9b. TWENTY-MILE BROOK (1060)



9c. LEE'S MILL STREAM (1100)



9d. LAZY MEADOW BROOK (1160)



9e. MONTHLY AVERAGE, 9 MAJOR SITES

Figs. 9a-e. Mean concentrations (% dry wt) of manganese for sampling stations 1030 (a), 1060 (b), 1100 (c), and 1160 (d) and mean monthly values for the nine major sampling locations (e). Vertical bar indicates $\pm$ one standard error of the mean.

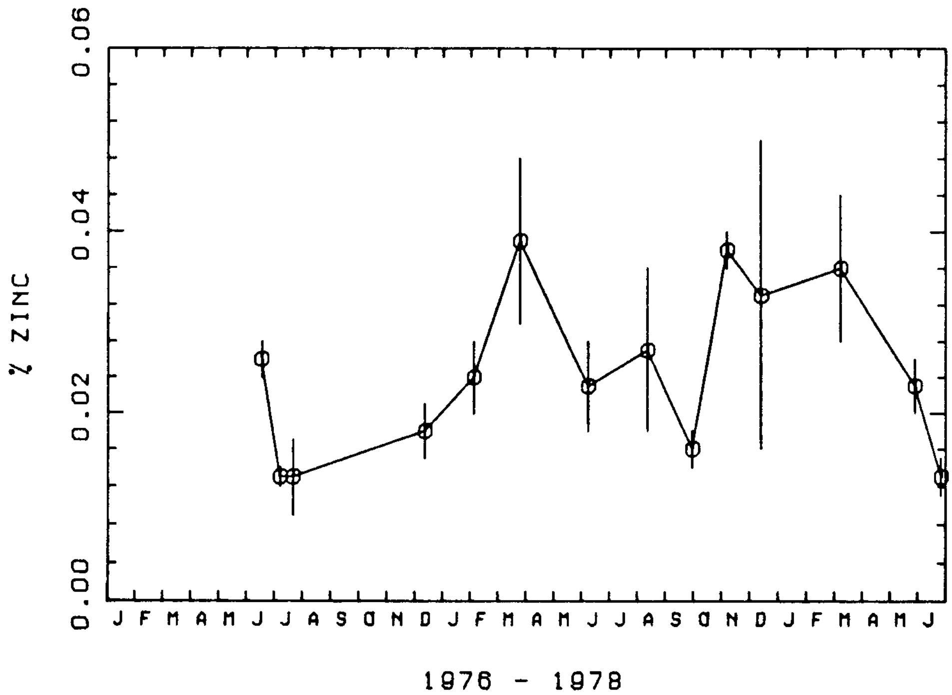
Spring values in *M. propinquum* and *M. elatinoides* shoots in New Zealand were 51 and 40 $ug.g^{-1}$, respectively (Rawlence and Whitton, 1977). Riemer and Toth (1969) reported whole mean plant concentrations of 307 $ug.g^{-1}$ in *M. spicatum* and 451 $ug.g^{-1}$ in *M. heterophyllum*. Boyd (1970) lists mean stem concentrations in September for *M. heterophyllum* at 54 $ug.g^{-1}$. In our study, the mean annual value was 170 $ug.g^{-1}$ (0.017%) in apices, which is similar to the 182 $ug.g^{-1}$ (Normandeau Assoc., 1977) and 218 $ug.g^{-1}$ (NHWSPCC, 1978) mean values, also reported from Lake Winnipesaukee. Our average monthly concentration values are in the range of 40 to 650 $ug.g^{-1}$ dry weight in the submersed apices with a seasonal pattern.

Seasonal minima of zinc occurred in the summer (Figures 10a-e). Carpenter and Adams (1977) observed a similar decline after May in *M. spicatum* shoots. The summer minima in the apices parallels the period of maximum stem elongation rates (Chagnon and Baker, 1979) and possibly is correlated with the interrelationship of the element with auxin (Nason and McElroy, 1963). Higher zinc concentrations were measured at sampling sites in the vicinity of marinas and urban runoff.

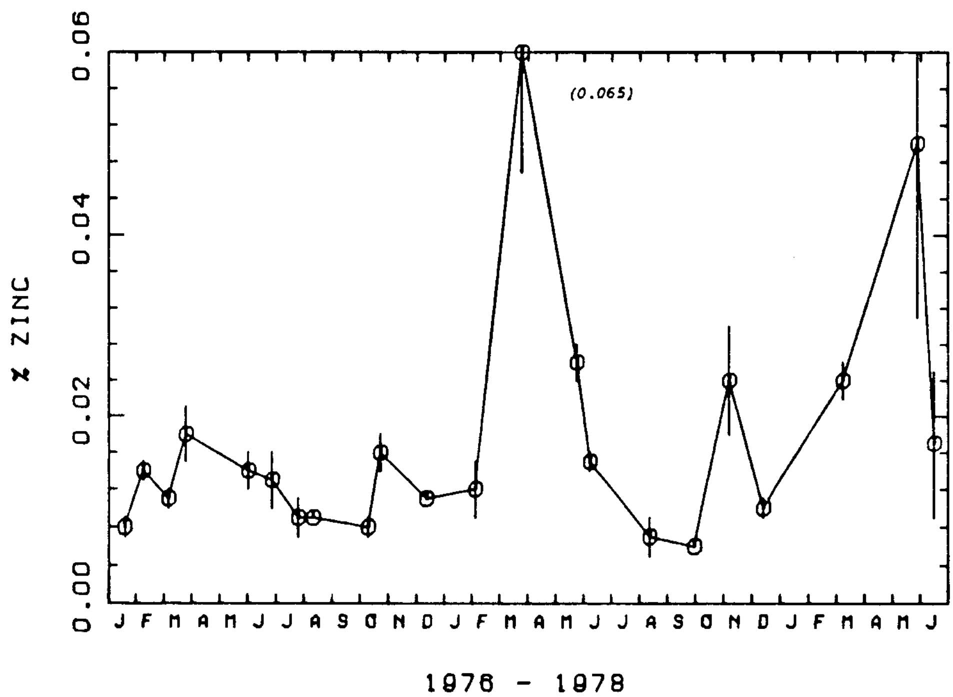
Copper

Copper is an essential micronutrient in plant metabolism as a component of the enzymes phenolase, laccase and ascorbic acid oxidase (Nason and McElroy, 1963). Like most metallic trace elements, copper in excess is toxic. The seasonal availability of copper as cuprous ion (Cu^{++}) in New England waters is quite low during the summer and reaches a maximum level in mid-winter (Kimball, 1973).

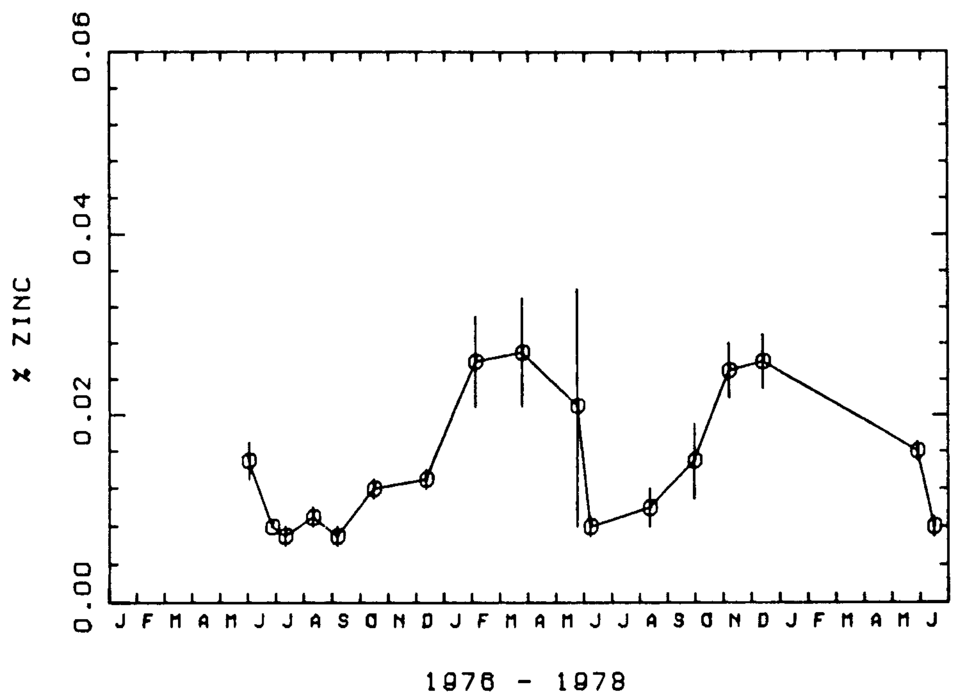
Copper concentrations in *M. heterophyllum* apices had no apparent seasonal trends or differences between sample sites. Apical tissue concentrations were from below the limit of detection (10 $ug.g^{-1}$) to 30 $ug.g^{-1}$. Partitioning of whole plants did not show significant differences in concentration between roots, stems, apices or flowers. These concentrations are lower than whole stem values reported for *M. heterophyllum* of 44 $ug.g^{-1}$ (Boyd, 1970), 39 $ug.g^{-1}$ (Riemer and Toth, 1969) and 42 $ug.g^{-1}$ (Normandeau Assoc., 1977) from Lake Winni-



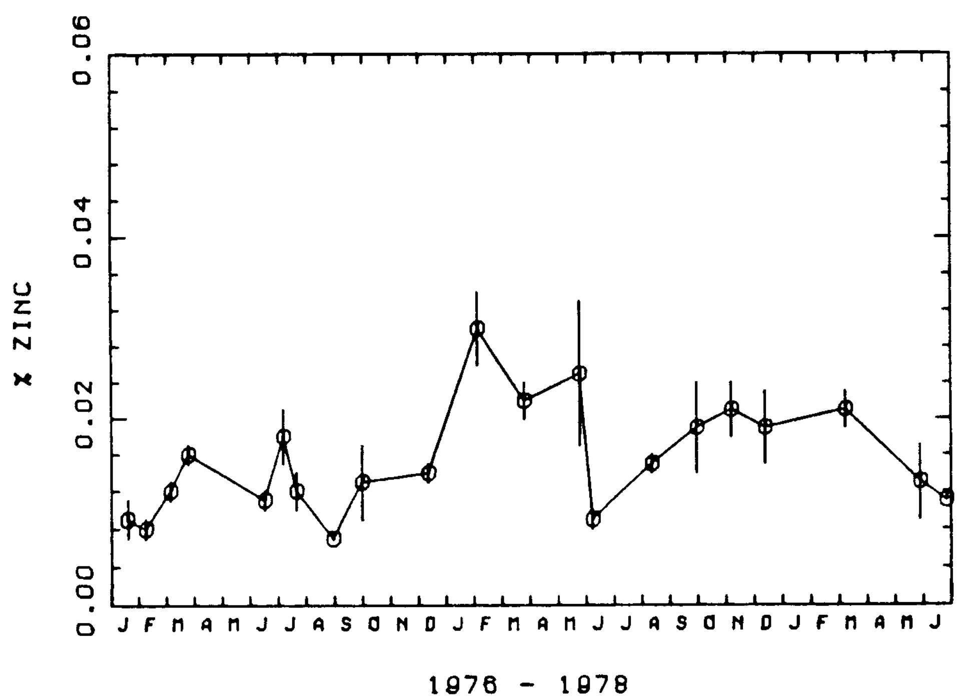
10a. OSTRAND'S MARINA (1030)



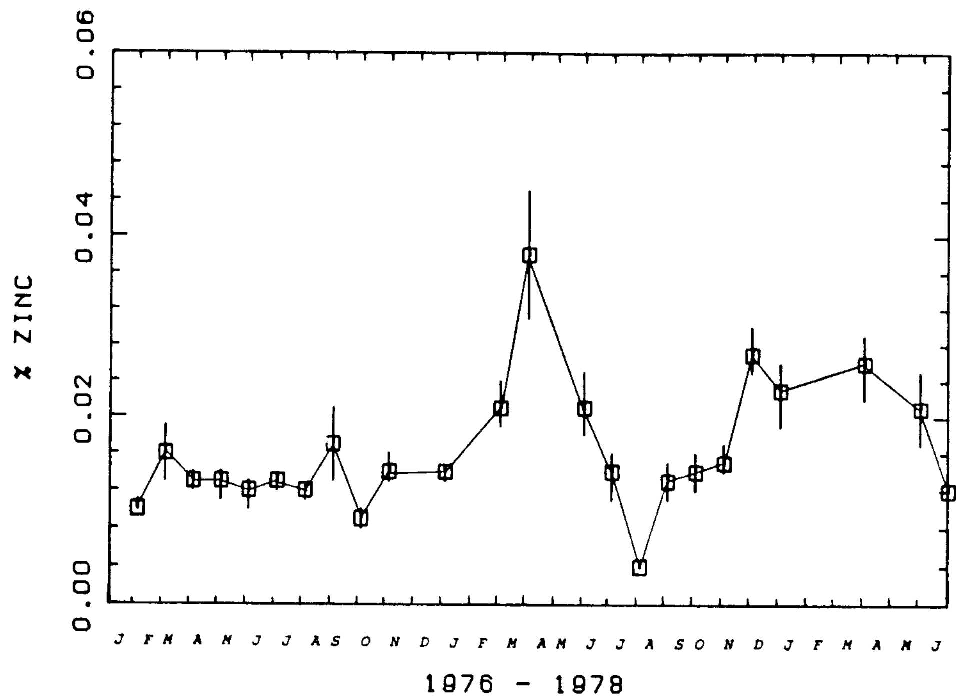
10b. TWENTY-MILE BROOK (1060)



10c. LEE'S MILL STREAM (1100)



10d. LAZY MEADOW BROOK (1160)



10e. MONTHLY AVERAGE, 9 MAJOR SITES

Figs. 10a-e. Mean concentrations (% dry wt) of zinc for sampling stations 1030 (a), 1060 (b), 1100 (c), and 1160 (d) and mean monthly values for the nine major sampling locations (e). Vertical bar indicates $\pm$ one standard error of the mean.

pesaukee. Values for whole stems in other members of the genus are 5 and 7 $ug.g^{-1}$ for M. propinquum and elatinoides, respectively (Rawlence and Whitton, 1977) and 26 $ug.g^{-1}$ for M. spicatum (Riemer and Toth, 1969). Carpenter and Adams (1977) reported whole-shoot copper concentrations from 7 to 19 $ug.g^{-1}$ during the growing season at 13 different sites for M. spicatum, with little variability between sites. Gerloff (1975) was unable to establish a growth-limiting role for copper in M. spicatum, and the copper requirement for Elodea occidentalis was very low. We concur with Gerloff's conclusion that low copper requirements may be an adaptation for aquatic plants to survive in soft-water, infertile lakes where copper availability is low.

CONCLUSIONS

The mineral concentrations in submersed apical tissues of *Myriophyllum heterophyllum* change seasonally. In part, the variations reflect seasonal differences in physiological requirements, reproductive state of the plant, synergistic interactions between nutrients, and relative availability of minerals in sediments and the water. The magnitude of the seasonal and spatial variations in mineral tissue levels in Lake Winnipesaukee is large (Table 3). Ash, phosphorus, the alkali metals - sodium and potassium, and the alkaline earth elements - calcium and magnesium, each vary by a factor (max/min) of three to five during an annual cycle. Typical spatial and temporal variations are much greater in the case of iron, manganese and zinc, with max/min ratios of 16 to 64.

Published attempts to correlate nutrient status of submersed aquatic macrophytes with their water environment have provided conflicting conclusions. Many authors have apparently assumed that the tissue chemistry in submersed aquatic macrophytes is primarily influenced by water chemistry, rather than sediment chemistry, and that the plants indulge in "luxury uptake", where excess supplies of elements occur. Our results question the practicality and validity of reported techniques which use mineral concentrations as an index of nutrient availability for plant growth (Gerloff and Krombholz, 1966) and as monitors of aquatic pollutants (Adams, Cole and Massie, 1973). While "luxury uptake" is a demonstrated phenomenon (Chagnon and Baker, 1979; Gerloff, 1977), the accumulation of mineral biomass is not necessarily in the same ratio that these minerals occur in the water. We conclude that mineral levels in the tissue of submersed plants have a marked variation, which to a large extent is influenced by changing physiological requirements with the seasons, rather than by seasonal changes in mineral availability in the water or sediment.

In addition, we conclude that there is a need to improve the existing data base used in making inter- and intraspecific comparisons

Table 3. Comparisons of Ash, Phosphorus and Cation Concentrations in *M. heterophyllum* Apices.

Parameter	General Seasonal Trend	Recurrent Seasonal Patterns[1]		magnified seasonal peak at tributary sites	% dry wt. range[2]	range max/min
		between years	between sites			
Ash	summer minimum	+	-	nd	9.1-30.2	3
P	summer minimum	-	-	nd	0.3-1.1	4
Na	summer maximum	+	+	nd	0.6-2.9	5
K	summer maximum	+	+	nd	1.1-4.4	4
Ca	no obvious trend	-	-	nd	0.5-2.2	4
Mg	no obvious trend	-	-	nd	0.09-0.43	5
Fe	late winter maximum	+	+	+	0.03-1.20	40
Mn	late winter maximum	+	+	+	0.01-0.64	64
Zn	summer minimum	-	-	nd	0.004-0.065	16
Cu	nd	nd	nd	nd	nd-0.003	nd

[1] recurrent seasonal patterns:
- (+) concentration pattern of the parameter is recurrent
- (-) concentration pattern of the parameter is variable

[2] calculated using monthly means from individual sampling sites

nd = not detectable

in the chemical composition of aquatic plants. Many comparative studies of mineral concentrations in the submersed plant tissue have ignored seasonal variation and type of tissue analyzed. Because of such deficiencies, the variability in the data defies interpretation (Hutchinson, 1975, Chap. 30). We recommend that future comparative studies include seasonal measurements on the different tissues, if the nutrient dynamics and interrelationships of rooted aquatic plants with water and sediment chemistry are to be understood.

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